The geography of species diversification

Alexander Lester Pigot

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Division of Biology, Imperial College London

Abstract

Speciation is largely a geographical process, but the role of geography in explaining patterns in species diversification remains poorly understood. Here I examine the effects of geographic ranges on the evolution of species diversity using a combination of phylogenetic and geographic approaches based on both simulated and real data.

In the first part of the thesis, I develop a neutral model combining the evolution of species' distributions and the geography of speciation to explore the effects of this relationship on the dynamics of species radiations. I show that neutral interactions between geographic ranges and speciation can lead to dramatic differences in diversity amongst clades and through time, and can mirror the phylogenetic patterns observed in real data derived from bird genera.

The evolution of ranges following speciation is likely to be a key factor in how patterns of species diversification unfold through time. In the second part of the thesis I examine the dynamics of ranges over both ecological and evolutionary timescales. First, using neutral and deterministic models of range expansion, I show that the structure of species' distributions in birds are highly deterministic and cannot be predicted by random ecological processes. I then use phylogenies of extant birds and mammals, to examine whether there is any evidence for systematic changes in range size through time. In both groups, I find that a model of random range evolution cannot be rejected. The results show that inferences regarding the dynamics of range evolution from extant phylogenies are likely to be confounded by the effects of speciation and extinction.

In the final part of the thesis, I test whether the geographic ranges of species determine the potential for speciation, focussing on how range shape constrains gene flow between populations. Using estimates of population neutral genetic differentiation for birds, mammals and amphibians, I find that differences in the degree of genetic cohesion of a species cannot be predicted by the shape of its geographic range. Hence, if range shape is to influence speciation it must do so through alternative mechanisms.

Taken together, these findings suggest that geography can have a profound effect on the patterns of diversification. Ignoring the role of geography may therefore result in misleading conclusions regarding the processes underlying variation in species diversity. While my findings show that geographic ranges are deterministic, they also imply that neutral processes may play a much larger role in the history of diversification than is generally appreciated. This geographical perspective therefore goes some way to reconciling the roles of neutrality and ecology in the evolution of species diversity.

Declaration

The work presented in this thesis is my own, with the following acknowledgements.

The avian geographic range data used throughout the thesis was provided by my supervisors, Prof I.P.F Owens and Dr C.D.L. Orme (both Imperial College London). My supervisors also provided considerable editorial input on all chapters, particularly Chapters 2 and 3 which have now been published in *Systematic Biology* (2010) 59: 660-673 and *Ecology Letters* (2010) 13: 705-715 respectively.

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Chapter 1

General introduction

1.1 Explanations for species diversity: chance, ecology and geography

Explaining why different groups of organisms vary so dramatically in species diversity remains one of the greatest challenges in evolutionary biology. Why for instance are there over a million species of insect but 'only' 10,000 species of birds, and why amongst birds are there so many species of passerines whereas there are so few species of ostrich of kagu (Anderson 1974; Raikow 1986; Willis 1922)? Over recent decades the explosion in the availability of molecular phylogenies has spurred a rapid growth in the number of studies addressing these kinds of questions (Barraclough et al. 1995; Davies et al. 2004; Isaac et al. 2005; Nee et al. 1992; Owens et al. 1999; Phillimore et al. 2006; Ricklefs 2003; Ricklefs 2007).

Some variation in diversity would be expected simply because of chance (Anderson 1974; Raup et al. 1973; Wright 1941; Yule 1925). This is because, even if the probabilities of speciation and extinction were equal across lineages, the stochastic nature of these events would mean that some groups would diversify more than others (Gould et al. 1977; Raup et al. 1973). However, studies comparing the diversity of taxonomic groups of similar age have shown that some clades contain far too many species, while

many others contain far too few, for it to be likely that such patterns have arisen purely by chance (Dial & Marzluff 1989; Guyer & Slowinski 1993; Heard 1992; Mooers 1995; Mooers & Heard 1997; Slowinski & Guyer 1989; Slowinski & Guyer 1993). As a result, deterministic processes appear to be required to explain variation in diversification.

Traditionally, explanations for differences in diversity have tended to focus on the role of ecology in promoting or limiting diversification (Darwin 1859; Schluter 2000; Simpson 1953; Stanley 1979). The idea that speciation is regulated by the processes of ecological divergence and niche filling continues to gain momentum and now provides a compelling framework for explaining variation in species diversity amongst groups and regions (Harmon et al. 2003; McPeek 2008; Phillimore & Price 2008; Rabosky 2009a; Rabosky & Lovette 2008; Rundle & Nosil 2005; Schluter 2001; Schluter 2009).

Darwin's finches have become widely celebrated as a classic example of such ecologically driven 'adaptive radiation' (Grant & Grant 2007). However, this group also provides a clear illustration of why such adaptive hypotheses are by themselves incomplete (Losos & Ricklefs 2009; Price 2008). For while finches have radiated into 14 species across the Galapagos Islands only a single species is found on the isolated Cocos Island. Explanations for this difference in richness must lie in the differing opportunities for geographical isolation across the Galapagos Islands compared to the lone Cocos Island (Mayr 1947).

Following decades of debate, it is now clear that most speciation events in animals require a period in which populations are geographically isolated, a model known as 'allopatry' (Barraclough & Vogler 2000; Coyne & Orr 2004; Coyne & Price 2000; Mayr 1942; Phillimore et al. 2008 but see Dieckmann & Doebeli 1999; Via 2001). The

occurrence of endemic species on islands (Mayr 1942), the absence of in-situ speciation on small islands and landmasses (Coyne & Price 2000; Kisel & Barraclough 2010; Losos & Schluter 2000), and the strong tendency for young sister species to occupy spatially non-overlapping distributions (Barraclough & Vogler 2000; Phillimore et al. 2008) all attest to the critical role of geographic isolation in speciation.

Ecological explanations for variation in the rate of species diversification often focus on the length of time required for speciation to be completed once geographical isolation has occurred (Rundell & Price 2009). For instance, strong divergent selection is expected to accelerate population divergence and the attainment of reproductive isolation compared to simply waiting for different mutations to arise (Coyne & Orr 2004; Gavrilets 2004; Schluter & Conte 2009). However, the potential influence of all these ecological and genetic processes is contingent on a period of geographic isolation in the first place. Variation in species diversification may therefore be largely dependent on the rate at which populations become geographically isolated.

1.2 Geography and species diversification

Geography has long featured prominently in explanations for species diversity (Brooks 1950; Cracraft 1982; Diamond 1973; Haffer 1969; Mayr 1942; Rosenzweig 1975). One set of explanations focusses on the aspects of the region within which a lineage occurs. For instance, particular geographical settings such as mountain ranges and island archipelagos may enhance rates of diversification due the abundance of geographic barriers (Davies et al. 2005; Hughes & Eastwood 2006; Owens et al. 1999; Phillimore et

al. 2007; Rahbek & Graves 2001; Rosenzweig 1995). Indeed, the latitudinal gradient in species diversity may be partly driven by the greater opportunities for populations to become spatially isolated in the tropics (Cardillo et al. 2005; Janzen 1967; Mittelbach et al. 2007; Terborgh 1973; but see Weir & Schluter 2007).

Another set of geographical explanations focus on the dynamics of species' ranges (Abe & Lieberman 2009; Barker et al. 2004; Jansson & Dynesius 2002; Moore & Donoghue 2007; Ricklefs 2003; Steeman et al. 2009). For instance, the opening and closure of gateways between ocean basins may have triggered pulses of speciation in whales (Steeman et al. 2009), while shifts in diversification rate in Dipsacales appear to be associated with episodes of expansion into new continents (Moore & Donoghue 2007).

Even where diversification appears to be driven by ecological shifts, the mechanism underlying this may be geographical (Cornell & Lawton 1992; Vamosi & Vamosi 2010). For instance, the evolution of resin canals in plants is regarded as a key innovation that promoted diversification by reducing attack by insect herbivores (Farrell et al. 1991). Although the connection between a reduction in predation and diversification remains unclear, one hypothesis is that enemy release leads to the expansion of geographic ranges and thus greater opportunities for geographic speciation (Farrell et al. 1991; Vamosi & Vamosi 2010). A similar geographic mechanism has also been put forward to explain why the evolution of phytophagy in insects has been followed by bursts of diversification (Cornell & Lawton 1992; Janz et al. 2006).

In addition to promoting diversification, geography has also been invoked in ecological models as a mechanism through which species diversity may be regulated (Rosenzweig 1975). As clades diversify, increasing competition between species may

result in a compression of their geographic ranges, thus reducing the opportunity for geographic isolation and further speciation (Phillimore & Price 2008; Phillimore & Price 2009; Price 2008; Rosenzweig 1975). By regulating the potential for speciation, the dynamics of geographic ranges may therefore provide a general mechanism explaining variation in diversification amongst lineages and through time (Jansson & Dynesius 2002; Price 2008; Rosenzweig 1975).

1.3 Geographic ranges and the opportunity for speciation

Underlying these geographical explanations are two central tenets. The first, and one that is widely accepted, is that a higher frequency of geographic barriers should promote diversification (Cracraft 1982; Davies et al. 2007; Davies et al. 2005; Fjeldsa & Rahbek 2006; Owens et al. 1999; Phillimore et al. 2007; Rahbek & Graves 2001; Rosenzweig 1995). The second is that the opportunity for spatial isolation is dependent on the size of the geographic range. While the expansion of a species should provide greater opportunities for populations to become geographically isolated (Abe & Lieberman 2009; Cornell & Lawton 1992; Farrell et al. 1991; Vamosi & Vamosi 2010), the restriction of a species to a small enclave should inhibit the potential for diversification (Price 2008; Rosenzweig 1975). Here, I review the mechanisms that are thought to underpin this relationship.

Geographic isolation between populations can arise through two mechanisms, termed ‘vicariance’ and ‘peripatry’ (Mayr 1982). In the vicariance model, changing

environmental conditions result in the geographic range splitting into separate fragments (Wiens 2004). This could be caused by geological events such as the separation of continents (Hedges et al. 1996) or advancing glaciers (Weir & Schluter 2004) or more subtle changes in habitat causing the local extinction of intervening populations (Kozak & Wiens 2006).

Rosenzweig (1975; 1978; 1995) argued that under this model, the chances of geographic isolation should increase with range size. While a widespread species is likely to be 'found' by geographic barriers arising across the landscape, these barriers are likely to 'miss' species with small ranges (Rosenzweig 1975; Rosenzweig 1995). He further argued that although extremely large ranges may be difficult to bisect by barriers, few if any species have ranges sufficiently large that this would occur (Rosenzweig 1978). Although this latter point remains debated, rates of vicariant speciation are generally expected to increase with range size, at least up to intermediate range sizes (Gaston 1998; Price 2008; Rosenzweig 1995).

Under the peripatric model, geographic isolation arises when rare long-distance dispersal events enable a species to expand its distribution across a pre-existing barrier, such as during the colonisation of an island (Mayr 1942; Mayr 1963). Although Mayr's (1942) model of founder speciation focused on the enhanced speed of population divergence in small peripheral isolates, the chance of forming these isolates in the first place is expected to increase with range size (Bellemain & Ricklefs 2008; Brown 1957; Vermeij 1987). Species with more extensive distributions and longer range perimeters are more likely to colonise new regions than those restricted to small habitats (Hubbell 2001;

MacArthur & Wilson 1967). An increase in range size is therefore also expected to increase the rate of peripatric speciation (Rosenzweig 1975).

It is also possible that geographic isolation could arise in the absence of barriers if the distance between populations is sufficiently large that gene flow between them is minimal (Endler 1977). This model, termed 'allo-parapatry', remains controversial because it is extremely difficult to rule out the existence of past geographic barriers (Irwin et al. 2001). Nevertheless, large range size is again thought to promote speciation through the reduction in gene flow and stronger divergent selection between populations at opposite ends of the range (Endler 1977; Kisel & Barraclough 2010; Wright 1943).

Mathematical models of parapatric speciation suggest that if large range size is associated with traits limiting population divergence (e.g. high dispersal), then the probability of speciation could actually decline with range size (Gavrilets et al. 2000). For this reason, a number of authors have suggested that range restricted species may be more prone to geographic isolation (Chown 1997; Jablonski & Roy 2003). All else being equal, however, theory suggests that the rate of speciation should increase with area (Endler 1977; MacArthur & Wilson 1967; Rosenzweig 1995).

1.4 Geographic ranges and the risk of extinction

Theory predicts that geographic range size should also influence rates of extinction, with higher extinction in populations with smaller ranges (Jablonski 1995). Indeed, range size is one of the strongest and most consistent predictors of rates of extinction in the fossil record and of extinction risk amongst contemporary taxa (Cooper et al. 2008; Jablonski

2008; Manne et al. 1999; Payne & Finnegan 2007; Powell 2007; Purvis et al. 2000). The relationship between range size and extinction risk could arise if widespread species possessed particular traits conferring resilience to environmental change, such as large population size, wide niche breadth or high dispersal ability (Hubbell 2001; Jablonski 2008). However, range size also appears to effect species survival independently of these factors (Jablonski & Hunt 2006; Powell 2007). For instance, large range size may reduce the chance that an environmental catastrophe eliminates all the populations across the range of a species (Rosenzweig 1995).

1.5 Outstanding questions

Despite often being invoked as a cause of variation in species diversity, the extent to which the dynamics of geographic ranges can explain differences in diversification across lineages remains poorly understood and the subject of ongoing debate (Gaston & Blackburn 1997; Phillimore & Price 2009; Price 2008; Ricklefs 2011). In the following section, I discuss some of the key reasons for this, and highlight those questions which I think need to be resolved in order for further progress to be made in this area.

How do ranges influence patterns of diversification?

An inevitable consequence of geographic speciation is that in the first instance, the distributions of the daughter lineages will each occupy only a subset of the parent range (Waldron 2007). The process of speciation therefore results not only in the multiplication

of species, but also in the division of geographic ranges (Chown 1997; Gaston 1998). Furthermore, one daughter lineage is likely to inherit a larger share of the parent range than the other, simply by chance (Anderson & Evensen 1978; Waldron 2007). In addition to dividing geographic ranges, speciation therefore also creates variation in range sizes amongst species (Anderson 1985; Gaston 1998). A similar effect of speciation on the distribution of species' abundances arises in Hubbell's (2001) neutral theory of biodiversity (Etienne et al 2007; Rosindell et al 2010).

This bi-directional process makes separating cause and affect in the relationship between speciation rates and range size problematic (Chown 1997). For instance, Phillimore et al (2006) showed that the average range size of species within bird families was negatively correlated with their richness. As the authors point out, this could be interpreted as evidence that speciation rates are higher amongst species with restricted ranges (see also Jablonski & Roy 2003). Alternatively this same pattern could arise if rapid speciation has resulted in the subdivision of species' distributions (Phillimore et al. 2006).

The effects of these reciprocal feedbacks on the dynamics of diversification remain largely unknown because most theoretical models of species diversification have been detached from this geographic context (Nee 2006; Raup et al. 1973; Yule 1925). While a number of studies have investigated the effects of evolving traits and speciation time-lags within these models, the implications of range dynamics have not been explicitly addressed (Agapow & Purvis 2002; Chan & Moore 1999; Heard 1996; Heard & Mooers; Losos & Adler 1995). Those models of species diversification that do involve a geographical component remain largely verbal (e.g. Diamond 1973; Phillimore & Price

2008; Rosenzweig 1995 but see Hubbell 2001). In order to understand the role of geographic ranges in species diversification, more quantitative models are required to elucidate the patterns expected to arise from these geographical processes.

What limits species' ranges?

If rates of diversification are determined by range size then a key question is what prevents species from expanding their distributions? Over evolutionary time scales, range limits are usually explained in terms of the failure of populations to adapt to the conditions beyond the range margin, due to processes such as genetic swamping or a lack of genetic variability (Blows & Hoffmann 2005; Holt 2003; Kirkpatrick & Barton 1997; Sexton et al. 2009). On ecological timescales, most studies have focused on identifying the specific environmental and biotic factors preventing species from expanding their distributions (Gaston 2003; Gaston 2009; Root 1988a; Root 1988b; Terborgh 1985).

The particular factors underlying range limits may have important consequences for the role of geographic ranges in diversification (Price 2008; Ricklefs 2010; Wiens & Donoghue 2004). If competition between closely related species limits range expansion then this could provide a way in which ecological processes may regulate diversity (Phillimore & Price 2009; Price 2008). Alternatively the geographic distributions of species may be largely independent of one another, each limited by a specific set of environmental factors and evolutionary adaptations (Colwell & Lees 2000; Gleason 1926; Ricklefs 2008). In this case, the historical processes determining species'

distributions may be more important for diversification than current ecological interactions (Barraclough et al. 1999; Wiens & Donoghue 2004).

Recently, neutral models have offered an alternative explanation for species' distributions (Bell 2001; Hubbell 2001). In these models, purely stochastic processes acting at the level of the individual, including point mutation, random death and dispersal, determine the population size and geographic distribution of a species (Hubbell 2001). Despite these seemingly unrealistic assumptions, these models are able to generate a number of macroecological patterns, including species-abundance relationships, species-area relationships and the hollow curve distribution of range sizes (Bell 2001; Hubbell 2001; Rosindell & Cornell 2009). Given the existence of these strongly divergent theories and there differing implications for the process of diversification, tests are required to elucidate the factors limiting species' ranges

How do ranges evolve through time?

If the chances of speciation and extinction depend on geographic range size then the effects of these processes on diversification are likely to depend on how ranges change through time (Gaston 1998). For instance, the repeated division of species' distributions may eventually lead to a halt in further diversification as the opportunities for geographic isolation are diminished (Price 2008). Only if species expand their distributions following speciation could the process of diversification be renewed (Diamond 1973; Phillimore & Price 2009; Price 2008). Alternatively, it has been argued that if geographic ranges fluctuate rapidly then differences in range size observed at any point in time would be

transient and could not lead to systematic variation in diversification across groups (Ricklefs 2010). In addition, such large fluctuations in ranges would tend to obscure any evidence for a relationship between range size and speciation amongst extant species (Gaston & Blackburn 1997; Losos & Glor 2003). Until the dynamics of species' distributions are better understood the role of geographic ranges in diversification will remain unclear.

Does range shape influence speciation?

In addition to differing in size, geographic ranges also vary widely in their shape (Brown & Maurer 1989; Brown et al. 1996; Rapoport 1982; Udvardy 1969). For instance, species occurring in regions of uniform climates may have relatively circular distributions while those occurring in regions of rapid environmental turnover may have more elongated ranges (Rapoport 1982; Ruggiero et al. 1998). In some cases this variation in range shape is extreme; Graves (1988) estimated that Andean birds have geographic ranges that are on average over 300 times as long as they are wide. A number of authors have speculated that variation in range shape could underlie differences in rates of diversification (Brooks 1950; Gavrilets & Losos 2009; Graves 1988). For instance, a long narrow range may be more likely to be fragmented by dispersal barriers than a compact distribution (Brooks 1950; Graves 1988; Rosenzweig 1978; Rosenzweig 1995). In addition, elongated ranges may reduce the levels of gene flow between populations (Gavrilets et al. 2000; Gavrilets & Losos 2009; Wright 1943). However, these mechanisms remain almost completely untested and so it is unclear what role, if any, range shape plays in diversification.

1.6 Outline of the thesis

In this thesis I attempt to address the outstanding questions identified in the previous section (Section 1.5) and thereby advance our understanding of the role of geographic ranges in species diversification. To do this, I use a combination of spatial and phylogenetic simulation approaches and data on the geographic distributions and phylogenetic relationships of real species. In Chapter 2, I develop a geographical model of diversification and use simulations to investigate the effects of geographic ranges on the dynamics of species radiations. I compare the results of these models to the geographic and phylogenetic patterns observed across a published dataset of bird phylogenies (Phillimore & Price 2008). In Chapters 3 and 4, I focus on a particular component of this model, the limits and dynamics of species' ranges, addressing this from two perspectives. First, in Chapter 3, I develop models of geographic range expansion and use these to test the role of neutral and deterministic processes in shaping current species' ranges in birds. Second, in Chapter 4, I test whether lineages undergo systematic changes in range size through time or whether range evolution occurs at random. To do this I assemble a database of avian and mammalian phylogenetic trees and compare the patterns in range size and evolutionary age to those expected under stochastic models of range evolution. In Chapter 5, I examine how the shape of species' ranges determines the potential for speciation. Compiling a geographical database of populations F_{ST} estimates across birds, mammals and amphibians I test whether the degree of genetic cohesion of populations can be predicted by the shape of their

geographic range. Finally, in Chapter 6 I discuss the principal findings of the thesis and offer some thoughts on their wider implications.

1.7 Caveats

Many of the caveats and assumptions present in this thesis are likely to be common to all studies using phylogenetic approaches to study diversification. These include the definition of species, methods of phylogenetic reconstruction, molecular dating, the choice of taxonomic scale and the reliance on correlative rather than experimental approaches (Agapow et al. 2004; Barraclough & Nee 2001; Bennett & Owens 2002; Harvey & Pagel 1991; Purvis & Agapow 2002). However, the analysis of geographic ranges poses some additional challenges. First, although maps of species' distributions are becoming increasingly available sufficient data to conduct large scale comparative analyses is still limited to a few "charismatic" groups. As a result, my analyses are restricted to terrestrial birds, mammals and amphibians for which data on the geographic distributions of almost all described species is available (Orme et al. 2005; Schipper et al. 2008; Stuart et al. 2004). Even though the specific findings may be restricted to these taxa, the major questions and approaches developed in this thesis could be applied to other groups as data on their geographic range becomes available. Second, most information on geographic ranges is in the form of hand drawn polygon maps representing the possible extent of occurrence (Gaston 1994). This type of data is only a crude abstraction of a much more complicated underlying structure (Brown et al. 1996; Hurlbert & Jetz 2007; Kunin 1998; Rapoport 1982). Because of these issues, I restrict my

analysis to the overall size and shape of species' ranges. The effects on diversification of other interesting properties of range structure, such as their fragmentation or aggregation (Pocock et al. 2006; Wilson et al. 2004), must await more accurate data. Finally, I restrict my study to breeding distributions. My justification for this is that the effects of range structure on the process of speciation are most likely to occur in the breeding range. Nevertheless, investigation of the effects of non-breeding distributions will be required for a complete understanding of how geographic ranges influence diversification (Bohning-Gaese et al. 1998; Lack 1971).

Chapter 2

The shape and temporal dynamics of phylogenetic trees arising from geographic speciation

2.1 Abstract

Phylogenetic trees often depart from the expectations of stochastic models, exhibiting imbalance in diversification amongst lineages and slowdowns in the rate of lineage accumulation through time. Such departures have led to a widespread perception that ecological differences amongst species or adaptation and subsequent niche filling are required to explain patterns of diversification. However, a key element missing from models of diversification is the geographical context of speciation and extinction. In this study, I develop a spatially explicit model of geographic range evolution and cladogenesis, where speciation arises via vicariance or peripatry, and explore the effects of these processes on patterns of diversification. I compare the results to those observed in 41 reconstructed avian trees. The model shows that non-constant rates of speciation and extinction are emergent properties of the apportioning of geographic ranges that accompanies speciation. The dynamics of diversification exhibit wide variation, depending on the mode of speciation, tendency for range expansion and rate of range evolution. By varying these parameters the model is able to capture many, but not all, of the features exhibited by birth-death trees and extant bird clades. Under scenarios with relatively stable geographic ranges strong slowdowns in diversification rates are produced, with faster rates of range dynamics leading to constant or accelerating rates

of apparent diversification. A peripatric model of speciation with stable ranges also generates highly unbalanced trees typical of bird phylogenies, but fails to produce realistic range size distributions amongst the extant species. Results most similar to those of a birth-death process are reached under a peripatric speciation scenario with highly volatile range dynamics. Taken together, the results demonstrate that considering the geographical context of speciation and extinction provides a more conservative null model of diversification, and offers a very different perspective on the phylogenetic patterns expected in the absence of ecology.

2.2 Introduction

Ecological processes have long been thought to be of fundamental importance in explaining the patterns of speciation and extinction amongst species and through time (Darwin 1859; Schluter 2000; Simpson 1953; Stanley 1979). For instance, competition and adaptation to available niches are thought to underpin the adaptive radiation of Darwin's finches (Grant & Grant 2007). However, it is also recognised that there may be a stochastic element to speciation and extinction rates (Gould et al. 1977; Raup et al. 1973), and disentangling the roles of ecological and stochastic processes in species diversification has become a central theme in macroevolution (Nee 2006). Studies invoking an influence of ecology on diversification are therefore often based on the statistical rejection of a purely stochastic model of diversification (Nee 2006).

The pure birth (Yule 1925) and birth-death (Kendall 1948) models have been the dominant null models in both paleontological and phylogenetic studies over the last three decades (Nee et al. 1994; Raup 1985; Ricklefs 2007). These models describe the branching of

phylogenetic trees, in which the probabilities of speciation and extinction are equal across lineages and constant through time (Gould et al. 1977; Nee 2006; Raup et al. 1973). Empirical studies have consistently revealed that observed clades of similar age often show a greater variance in species richness than expected under an equal rates model (i.e., phylogenetic trees are unbalanced) (Blum & Francois 2006; Mooers & Heard 1997; Slowinski & Guyer 1993). This finding has, therefore, often been interpreted as evidence that ecological differences among lineages must underpin variation in speciation and extinction rates (Dial & Marzluff 1989; Owens et al. 1999; Ricklefs 2004; Slowinski & Guyer 1993). Another set of predictions, which arise from the constant rate model, concerns the accumulation of lineages on a reconstructed phylogeny through time. On a logarithmic scale the number of species increases linearly with time under a pure birth model or shows an upturn toward the present under a birth-death model where death is non-zero (Nee 2006; Nee et al. 1992; Ricklefs 2007). In contrast, numerous studies of real reconstructed phylogenies have found that, in many clades, lineage accumulation was initially rapid but has declined toward the present (McPeek 2008; Nee et al. 1992; Phillimore & Price 2008; Rabosky & Lovette 2008; Seehausen 2006; Weir 2006; Zink & Slowinski 1995). Further evidence for temporal heterogeneity in speciation and extinction rates comes from the lack of correlation between clade age and clade richness in many taxa (Rabosky 2009b). Although a multitude of processes may explain heterogeneity in diversification rates, this departure from the predictions of constant rate models is often taken as evidence for the saturation of niche space and limits to diversity (Phillimore & Price 2008; Weir 2006).

The use of the birth-death process, however, extends beyond null models, permeating many aspects of macroevolutionary research (Nee 2006). Estimating the history of

diversification from neontological phylogenies (i.e. those based on extant lineages alone) requires an underlying model of diversification (Ricklefs 2007) and the birth-death model has often been used to infer speciation, extinction and diversification rates using branching times (FitzJohn et al. 2009; Nee 2001), the age and diversity of the clade (Nee 2001; Ricklefs 2007; Yule 1925), or terminal branch lengths (Weir & Schluter 2007). Finally, the birth-death model is also assumed in some Bayesian phylogenetic reconstruction approaches, in which a constant rate process provides a prior distribution for branching rates (Drummond & Rambaut 2007).

Although the simplicity, mathematical tractability and apparent transparency of the birth-death model have probably contributed to its continued popularity (Nee 2006), a key element missing from current null models of diversification is the geographical context of speciation. For most animal species at least, the fundamental requirement for speciation is the occurrence of geographical isolation and reduction in gene flow between populations (allopatric or peripatric speciation) (Coyne & Orr 2004). The splitting of a lineage in a phylogenetic tree occurs alongside the splitting of its distribution in space. Speciation therefore not only adds to the number of species within a clade, but also simultaneously alters the distribution of geographic range sizes across lineages and through time (Gaston 1998; Waldron 2007). This is important, because the geographic range size of a lineage is likely to constrain the probabilities of further speciation and extinction (Rosenzweig 1975). All else being equal, larger areas will offer greater opportunities for geographical isolation due to a higher incidence of dispersal barriers, greater habitat heterogeneity and the limits to gene flow (Gavrilets et al. 2000; Kisel & Barraclough 2010; Rosenzweig 1978). Large ranges also provide a buffer against stochastic or environmentally driven fluctuations in size that may lead to extinction (Jablonski 1995). Here, I develop a model of diversification that explicitly incorporates the

processes of geographical isolation and range dynamics underlying the birth and death of lineages and examine the extent to which the inclusion of these processes can account for the "non-random" patterns observed in phylogenetic trees. I first explore the phylogenetic and geographic patterns of clades expected under this model and then compare these patterns to those (i) generated under birth-death models and (ii) observed in real avian phylogenies.

2.3 Methods

To investigate the effects of the geography of speciation and extinction on cladogenesis, I simulated a process of species diversification using spatially explicit models of species' ranges through time (Figure 2.1). My approach builds on earlier simulation studies that have addressed the geography of speciation (Barraclough & Vogler 2000; Phillimore et al. 2008) and the heritability of geographic range size (Waldron 2007). The model is both neutral and non-interactive, in that the dynamics of species' ranges are specified from a single distribution (Hubbell 2001) and I assumed no interactions amongst taxa or limits to the number of potentially coexisting species (MacArthur & Wilson 1967). I regard these conditions as the most sensible and transparent starting point for a geographic model of diversification in which the role of ecology is excluded. Each simulation started with a continuous square domain with side lengths of 500 units containing a single species, represented by a square range with sides of 150 units (9% of the domain). I note that the results were not qualitatively altered when using a larger starting range size of 350x350 units (49% of the domain) and so I only discuss those results pertaining to the smaller starting range size. The position of the range was

randomly assigned by drawing the coordinates of the range centroid from a uniform distribution and discarding those ranges which crossed the domain boundary (Figure 2.1a).

2.3.1 Simulating range dynamics

Geographic ranges are dynamic through time, shifting in their size, shape and position (Liow & Stenseth 2007; Ricklefs & Cox 1972). I simulated these dynamics by adding a random normal deviate to each edge of each rectangular species' range at each time step with each simulation lasting for 2000 time steps, allowing the boundaries of the species' range to drift independently of one another across the landscape (Barraclough & Vogler 2000; Phillimore et al. 2008) (Figure 2.1b). I initially assume that range boundaries fluctuate idiosyncratically through time, and thus in the baseline simulations set the mean of the normal deviate (μ) to 0. I therefore model the location of range boundaries as evolving under a Brownian process, a simplification that may be appropriate if ranges are limited by the independent variation in a large number of environmental and evolutionary factors (Colwell & Lees 2000; Ricklefs 2008). Fluctuations in species' ranges can occur rapidly (Davis & Shaw 2001) relative to the lengths of time required for speciation (Weir & Schluter 2007) but there is little empirical evidence on typical rates of range size evolution across clades. I therefore explored arbitrary levels of range dynamism by modifying the variance of the random normal deviate (σ^2) from which changes in range boundary position are drawn (values: 0.05, 2.5, 5, 7.5 and 10): when $\sigma^2 = 10$, 50% of range edges advance or retreat by more than 2.13 spatial units per time unit. I note that although faster rates of range evolution are possible, the effects of range dynamism on the patterns of diversification were evident within the range of parameter values explored. Given the suggested importance of range expansions in determining slowdowns in

diversification rate (Phillimore & Price 2009), I also explored scenarios where ranges had a tendency to expand by altering the mean of the random normal deviate from 0.025 to 0.6 (values: 0.025, 0.05, 0.075, 0.1, 0.2, 0.4, 0.6).

Random fluctuations in species' range boundaries leads to changes in geographic range size, which evolves according to the product of the summed normal deviates of opposite range boundaries. This may eventually result in the range size of a species drifting to zero, whereupon the species becomes extinct (Figure 2.1d). Extinction is therefore an emergent property of range dynamics and is most likely when μ is low and σ^2 is high. Because the dynamics of species' ranges occurred in discrete time, this will tend to underestimate the extinction rate compared to when ranges fluctuate continuously, because in the latter case species could have drifted to extinction during the intervening period. To minimise the extent which extinctions were underestimated, I therefore simulated range movement at a temporal resolution that exploratory simulations showed was sufficient for the number of missed extinctions to stabilise at a low value under the range of parameter values I explored.

The edge of the domain represented a hard boundary and ranges that extended beyond the domain boundary were immediately truncated (Barraclough & Vogler 2000). I regard this scenario as more closely resembling the geometric constraints on species' ranges than assuming either a torus or an infinite domain (Hubbell 2001). In the simulations time is not absolute but is instead set by the relative rates of range movement and speciation and doubling the length of the simulation, for instance, is equivalent to doubling the rate of range movement and speciation. However, I envisage a single time unit as corresponding to a period on the order of 10^5 years and other parameters were chosen to give biologically plausible rates of extinction and speciation within this timeframe. I did not investigate other, more complex,

models of range size evolution (Liow & Stenseth 2007) because theoretical explanations for these dynamics are generally based on non-neutral, ecological processes (Ricklefs & Bermingham 2002).

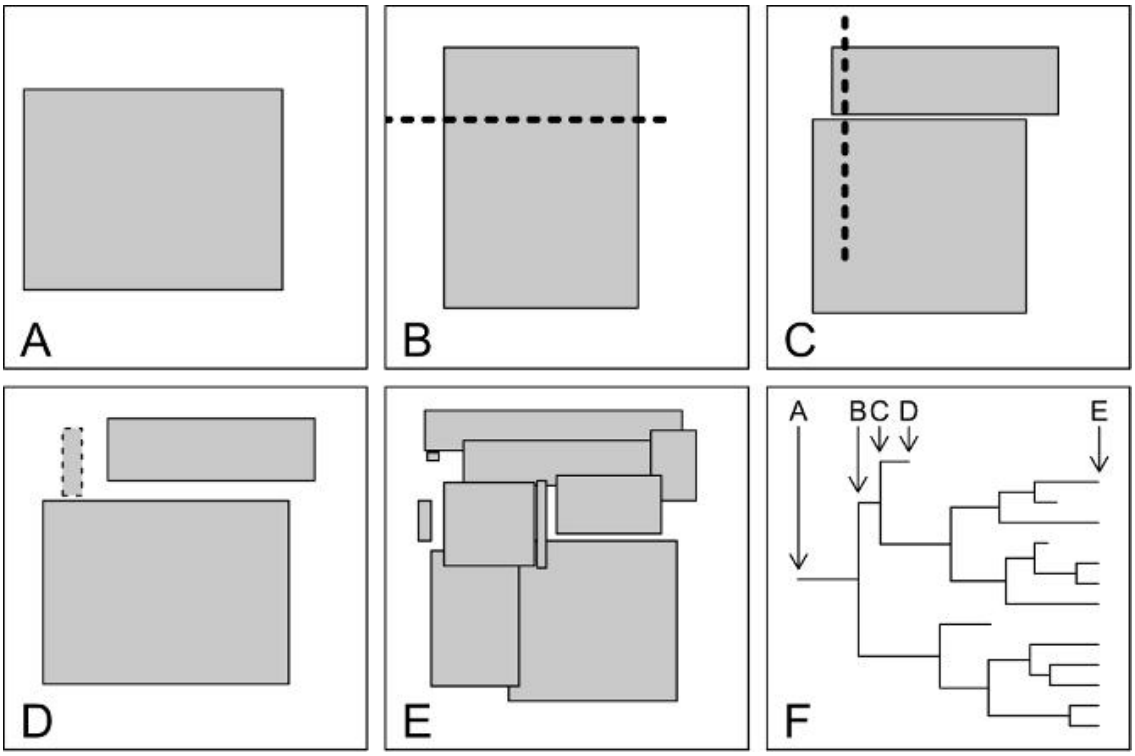


Figure 2.1. Example geographical model of cladogenesis under the vicariance speciation scenario at 5 time points. a) A single species' range (grey rectangle) is randomly placed in the square domain. b) The species' range has undergone random range movements. A barrier (black dashed line) is randomly dropped on the domain bisecting the range resulting in the formation of two sister species. c) The two species' ranges have undergone random independent range movements. A second barrier is dropped bisecting one of the species' ranges but missing the other, resulting in a single speciation event. d) The range of one of the newly formed sister species has drifted to extinction (dashed rectangle). e) Continued range movement and successive rounds of speciation result in a clade of species, giving f) the corresponding phylogeny at the end of the simulation.

2.3.2 Simulating speciation

For most animal species, some form of geographical isolation between populations appears to be required for speciation (allopatric or parapatric speciation) (Coyne & Orr 2004). New species arose in the simulations either by a barrier bisecting the existing distribution of a species (vicariance) or from dispersal to a new location (dispersal or peripatric speciation). Under both scenarios, the probability of speciation arose as an emergent property of the model. Multiple species could speciate in a given time step, either through the bisection of multiple species' ranges or the simultaneous production of dispersal events, with speciation treated as an instantaneous event. Although the assumption of instantaneous speciation is a simplification (Losos & Adler 1995), this approach can be thought of as modelling only those instances where geographical isolation persisted for long enough to cause speciation. Following speciation, the ranges of the daughter species moved independently of one another and could each undergo subsequent speciation events or go extinct (Figure 2.1d). Although here I focus on an allopatric model of speciation, I expect that a parapatric scenario, in which reproductive isolation arises in the absence of complete geographic isolation (Coyne & Orr 2004), would produce results qualitatively similar to the vicariance model. This is because both models result in the splitting of an ancestral species' range regardless of whether this occurs due to a dispersal barrier (vicariance) or selection across a steep environmental gradient (parapatry). Under both speciation models I discarded simulations in which fewer than eight species survived to the last time step, equal to the minimum number of species observed within the selection of bird genera.

Vicariance: In the vicariance scenario, I modelled geographic barriers by randomly dropping line segments onto the domain (Rosenzweig 1978) (Figure 2.1b). Barriers could miss a species' range, pass only part of the way through it, or bisect it, with only the latter resulting in speciation (Rosenzweig 1978) (Figure 2.1c). Barriers were dropped on the domain following a waiting time drawn from an exponential distribution (mean = 20 time units), rounded to the nearest time step, consistent with barriers arising via a Poisson process of constant rate per unit time. Barriers were removed immediately so that range dynamics could proceed unimpeded. The coordinates for the centroid of each barrier within the domain was randomly drawn from uniform distributions. The orientation of the barrier was assigned as horizontal or vertical randomly and with equal probability; all ranges consequently retain a rectangular form. Barriers were allowed to extend beyond the domain to minimise the tendency for a mid-domain effect in the frequency of barriers (Colwell & Lees 2000). Although barriers will still tend to overlap more at the centre of the domain than at the edges, this is mitigated by the random placement of the species' range at the start of the simulation.

The length of the barriers was drawn from a uniform distribution, in the range 0-550 so that species covering the entire domain had a non zero probability of speciation ($p = 0.0003$). In accordance with previous modelling results (Rosenzweig 1978), the probability of speciation in the vicariance model peaks at intermediate range sizes (Figure 2.2). For square ranges, the peak probability ($P = 0.005$) of speciation occurs when ranges occupy approximately 20% of the domain (Figure 2.2a). This is because, as the size of the range increases, species are more likely to encounter barriers but fewer of the barriers will be sufficiently long to completely bisect the range (Figure 2.2a) (Rosenzweig 1978). The shape of the relationship between range size and the probability of bisection is sensitive to the

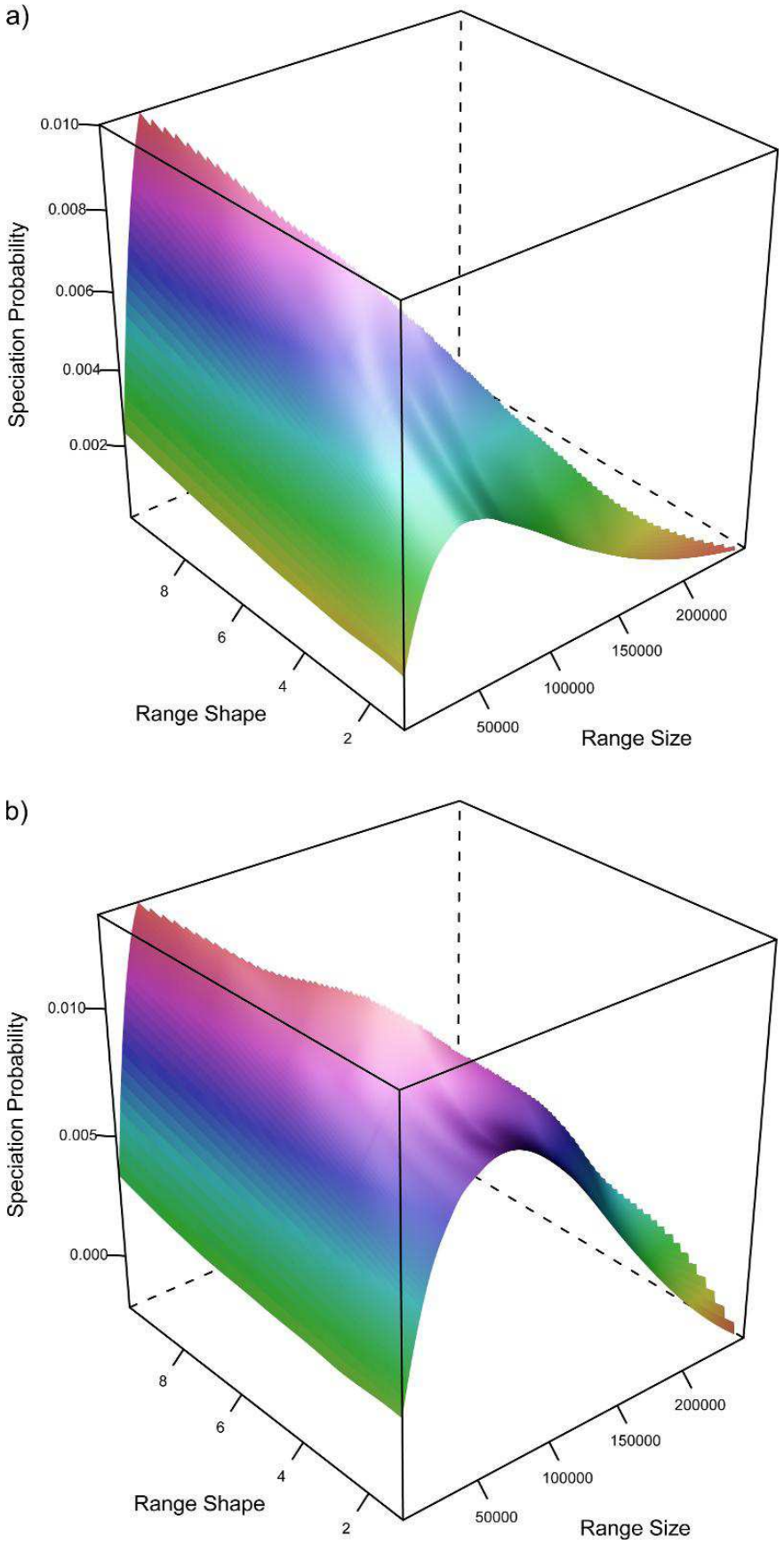
distribution of barrier lengths and so I also examined the consequences of using an exponential distribution of barrier-lengths whereby most barriers were short (mean length=110 spatial units) (Appendix 1 Figure S1a). In this case, the probability of speciation is reduced, with the peak probability (P = 0.0008) corresponding to a smaller range size (occupying approximately 10% of the domain) (Appendix 1 Figure S1a). The probability of range bisection is also modulated by range shape; increasing the length to width ratio of the range increases the chance of being bisected (Figure 2.2a). Range shape is particularly important when most barriers are small relative to the size of species' ranges (Appendix 1 Figure S1a).

Peripatry: I simulated dispersal speciation such that, at each time step, each extant species could give rise to a new peripatric species. The probability of producing a peripatric species is expected to be linearly related to either the perimeter or the area of the geographic range, depending on the relative range width and the average dispersal distance (MacArthur & Wilson 1967). Because the size and shape of the species' ranges varied in the simulations, for consistency I modelled the probability of dispersal as the range perimeter expressed as a proportion of the domain perimeter. Qualitatively similar probabilities were obtained if the proportional area was used (Appendix 1 Figure S1b). When a species was found to have dispersed, a dispersal direction was selected perpendicular to a randomly selected point along the range perimeter, thus favouring dispersal perpendicular to the long axis of a range. The dispersal distance away from the parent range was drawn from an exponential distribution with a mean of 100 and hence a median dispersal distance of approximately 69.3 spatial units. The point identified was used as the centroid of a new species' range with edge lengths drawn from a normal distribution (mean=25, sd=5). If the colonist occurred near the edge of the domain I

truncated its distribution so that it occurred entirely within the domain; if the new range fell entirely outside the domain, the speciation event was assumed to have failed. Ranges occurring near the edge of the domain have a lower chance of producing peripheral isolates because they are more likely to lose colonists beyond the domain edges. The random placement of the species' range at the start of the simulation means that this will not lead to bias across models.

In the peripatric model, speciation probability is also a peaked function of range size, with the maximum probability of speciation (P = 0.01) occurring when ranges covered approximately 28% of the domain (Figure 2.2b). This occurs because although dispersal probability approaches 1 for the largest ranges an increasing proportion of these events fall beyond the boundary of the domain. I also investigated the case where the probability of dispersal was proportional to the area of the range rather than the perimeter (Appendix 1 Figure S1b). Where the probability of speciation is proportional to perimeter length, range shape alters the speciation probability because elongated ranges have a higher perimeter to area ratio (Figure 2.2b).

Figure 2.2. On the following page. The relationship between range size (units^2), range shape and the probability of speciation under the a) vicariance model with a uniform distribution of barriers lengths (0-550) and b) dispersal model where the probability of producing a colonist is linearly related to the range perimeter expressed as a proportion of the domain perimeter. Smooth surfaces were fitted using a loess model with a span of 0.4. Range shape is measured as the relative length of the range long and short axis, with higher values indicating more elongated ranges. I did not plot length to width ratios greater than 10 because given the geometric constraints imposed by the domain boundaries most parameter space would be empty.


a)
Speciation Probability
0.010
0.008
0.006
0.004
0.002
Range Shape
8
6
4
2
Range Size
50000
100000
150000
200000
b)
Speciation Probability
0.010
0.005
0.000
Range Shape
8
6
4
2
Range Size
50000
100000
150000
200000

2.3.3 Phylogenetic tree shape and clade patterns

For each of the 240 combinations of parameter values I performed 200 simulations, recording: the timing of all speciation and extinction events; the coordinates of the species' ranges at the end of the simulation; and the phylogenetic relationships amongst species (Figure 2.1f). From the complete phylogeny including extinctions, I extracted the reconstructed phylogeny by retaining only those branches leading to extant tips. Clade size was recorded as the number of extant species and varied greatly between simulations. I therefore measured the imbalance of the reconstructed trees using the β tree-splitting parameter, which is independent of clade size and, in contrast to other clade imbalance statistics, does not assume a particular model of cladogenesis (Aldous 1996). Code to implement the β tree-splitting parameter was provided by M. Blum (Blum & Francois 2006). Due to computational limits I did not calculate imbalance for trees containing more than 10,000 extant species, but because this occurred in only 104 of the 48,000 trees, this is unlikely to bias the results. Finally, I recorded the range size of the extant species and calculated the proportion of the domain occupied by each species, the skew (g) in the range size frequency distribution for each clade, and the phylogenetic signal in range size using Pagel's lambda (λ) (Pagel 1999): λ varies between 0 and 1, with $\lambda = 1$ consistent with a Brownian model, and $\lambda = 0$ indicating that the trait varies at random with respect to phylogeny (Freckleton et al. 2002).

I measured temporal shifts in diversification rate (ρ) as the proportional difference in rate between the first (r_1) and second (r_2) half of the reconstructed phylogeny ($\rho = (r_2 - r_1)/(r_1+r_2)$). The rate within each half, split at the midpoint between the tips and the crown group divergence, was calculated as $r = (\log(n_2)-\log(n_1))/t$ (Magallon & Sanderson 2001), where n_1

and n_2 are the number of extant species at the start and finish of the time period and t is its length. The parameter ρ varies from -1 to 1, with ρ = 0 indicating constant diversification rates, ρ > 0 indicating a speedup in diversification rate, and ρ < 0 indicating a slowdown in diversification rate towards the tips of the tree. I implemented this method in preference to the γ statistic (Pybus & Harvey 2000) because γ exhibits scaling with clade size when changes in diversification rate are not constant (McPeek 2008).

2.3.4 Bird trees and birth-death models

To examine how the geographical models departed from constant rate models, I compared β and ρ from the simulations with that predicted by the birth-death model, under a variety of extinction rates (b=0.2, d=0, 0.05, 0.2), run for 20 time steps. Finally I compared the results of the geographical model to the imbalance and temporal diversification in 41 species level bird phylogenies taken from Phillimore and Price (2008). These phylogenies, at or around the genus level, typically contained more than 80% of the recognised species from the clade. To examine the effects of incomplete sampling, I randomly removed 20% of the species from the simulated trees and recalculated tree imbalance and the shift in diversification rate. This did not qualitatively alter the conclusions and so I focus on the results from the complete clades (Appendix 1 Figures S2). Following Phillimore and Price (2008), only lineages up to the last bifurcation event prior to 2 Mya were counted when estimating the shift in diversification rate because more recent splitting events may not be recorded as different species (Purvis et al. 2009). I calculated the range size of the species in the bird trees using a global database on avian breeding distributions (Orme et al. 2005) according to the standard avian taxonomy of Sibley and Monroe (1990). I used the combined area of the biogeographic realms (Olson et al.

2001) within which a species was distributed as a measure of domain size, and for each clade calculated the average proportion of the domain occupied by each species. Finally, I calculated the skew in the range size frequency distribution and the phylogenetic signal (λ) in range size (Pagel 1999) of each clade. Due to computational limits, λ was not calculated for trees containing more than 1000 extant species.

2.4 Results

2.4.1 Temporal dynamics of species richness and range size

In the simulated clades the phylogenetic patterns of diversification are determined by an interaction between the dynamics of species' ranges and the geographic mode of speciation. Whether through the bisection of geographic ranges (vicariance model) or the budding of small peripheral isolates (peripatric model), speciation leads to a reduction in geographic range size between parent and the average of the daughter lineages. When ranges have either no or little tendency to expand (μ=0-0.05), this successive apportioning of species' distributions results in a rapid decline in range size through time. Clades which by chance experience rapid diversification become characterised by more restricted ranged species, resulting in a strong negative relationship between clade richness and geographic range size (Figure 2.3). By the end of the simulations the median range of the extant lineages typically covers less than 5% of the available area (Figure 2.4g-j). Consequently, although speciation probability is a peaked function of range size, the restricted nature of most geographic ranges means that for the majority of species, reductions in range size generally lead to lower probabilities of speciation.

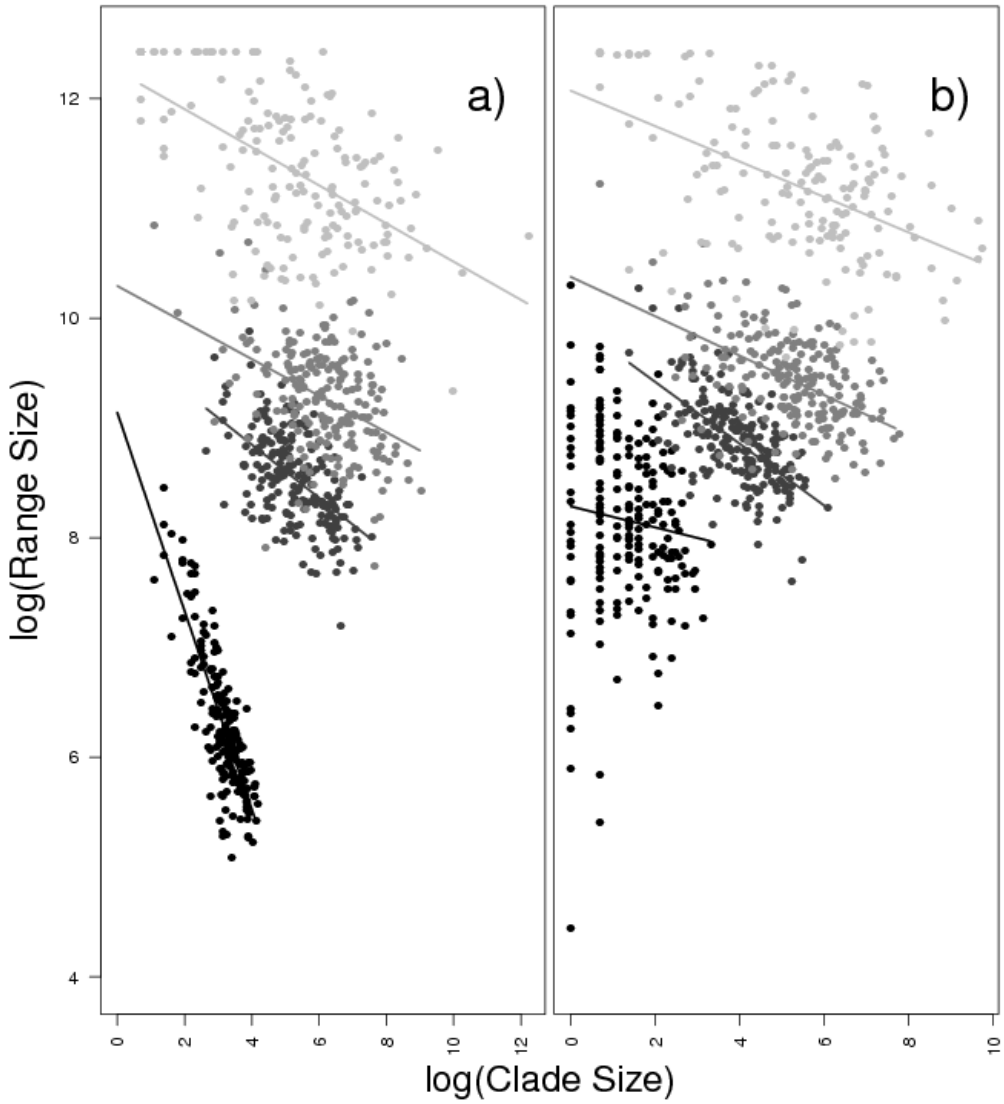


Figure 2.3. Median range size against clade richness under the vicariance model, under a) low (σ^2 =0.05) and b) high (σ^2 =5) variance in range movement. Dark grey to light grey points represent different rates of range expansion (μ) (0, 0.05, 0.1 and 0.2).

Declining range sizes lead to negative values of ρ, indicating strong temporal slowdowns in the net rate of diversification. This is particularly apparent under the vicariance model (Figure 2.5i), where levels of ρ are similar to the strongest declines in diversification rate found in the selection of bird genera (Figure 2.5g). In contrast, under the birth-death model only constant or accelerating diversification rates are predicted, depending on the relative extinction rate (Figure 2.5h). When ranges have a stronger tendency to expand, this counteracts the trend toward smaller range sizes (Figure 2.3), increasing the diversification rate and leading to larger clade sizes. When the rate of expansion balances the decline in range size caused by speciation, temporally homogenous diversification rates occur (Figure 2.5i,k). At the highest rates of range expansion that I explored (μ=0.4, 0.6), however, geographic ranges tend to fill the domain, reducing the probability of speciation and leading to strong temporal slowdowns in the net rate of diversification (Figure 2.5i).

When rates of range movement are high (σ^2=5), species with restricted ranges rapidly become extinct, resulting in smaller clade sizes (Figure 2.4b-e) and an increase in average range size (Figure 2.3). These high rates of extinction lead to an apparent acceleration in the rate of diversification through time (Figure 2.5j,l). A strong tendency for range expansion prevents small ranged species from going extinct, so that diversification returns to a more constant rate through time (Figure 2.5j,l). Under both speciation models, values of ρ most consistent with that observed amongst bird genera, occur under low rates of range expansion (μ=0.05) and little stochasticity in range edge movement (σ^2=0.05).

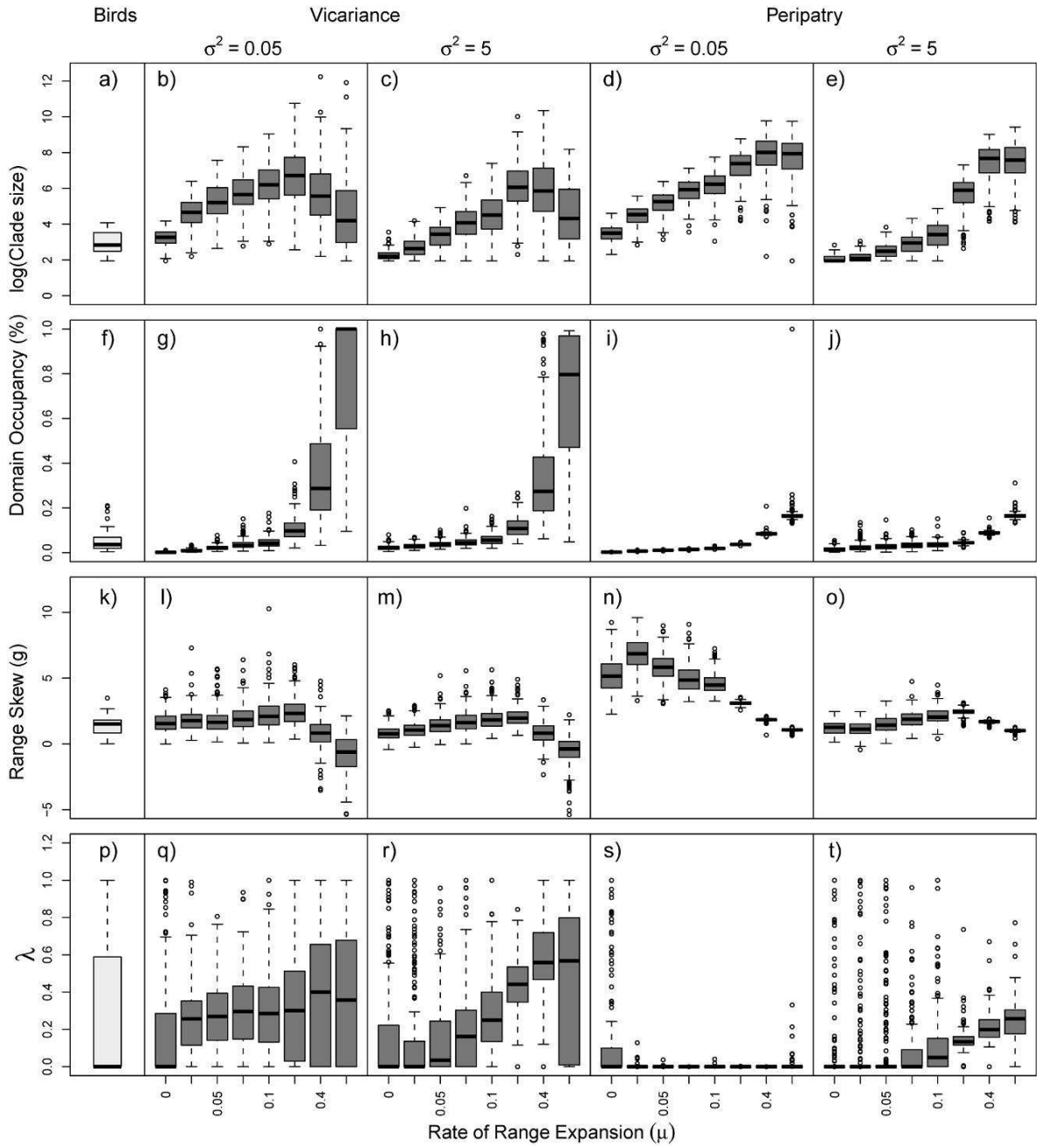


Figure 2.4. Log clade species richness (a-e), median proportion of domain occupied (f-j), skew in range size distribution (k–0) and Pagel's lambda (λ) (p-t) for bird genera (a,f,k,p) and the geographical model (b-e, g-j, l-o, q-t). The modelled simulations show variation arising from different speciation modes (vicariance or peripatric), different range movement variance (σ^2 = 0.05 and 5) and rates of range expansion (μ).

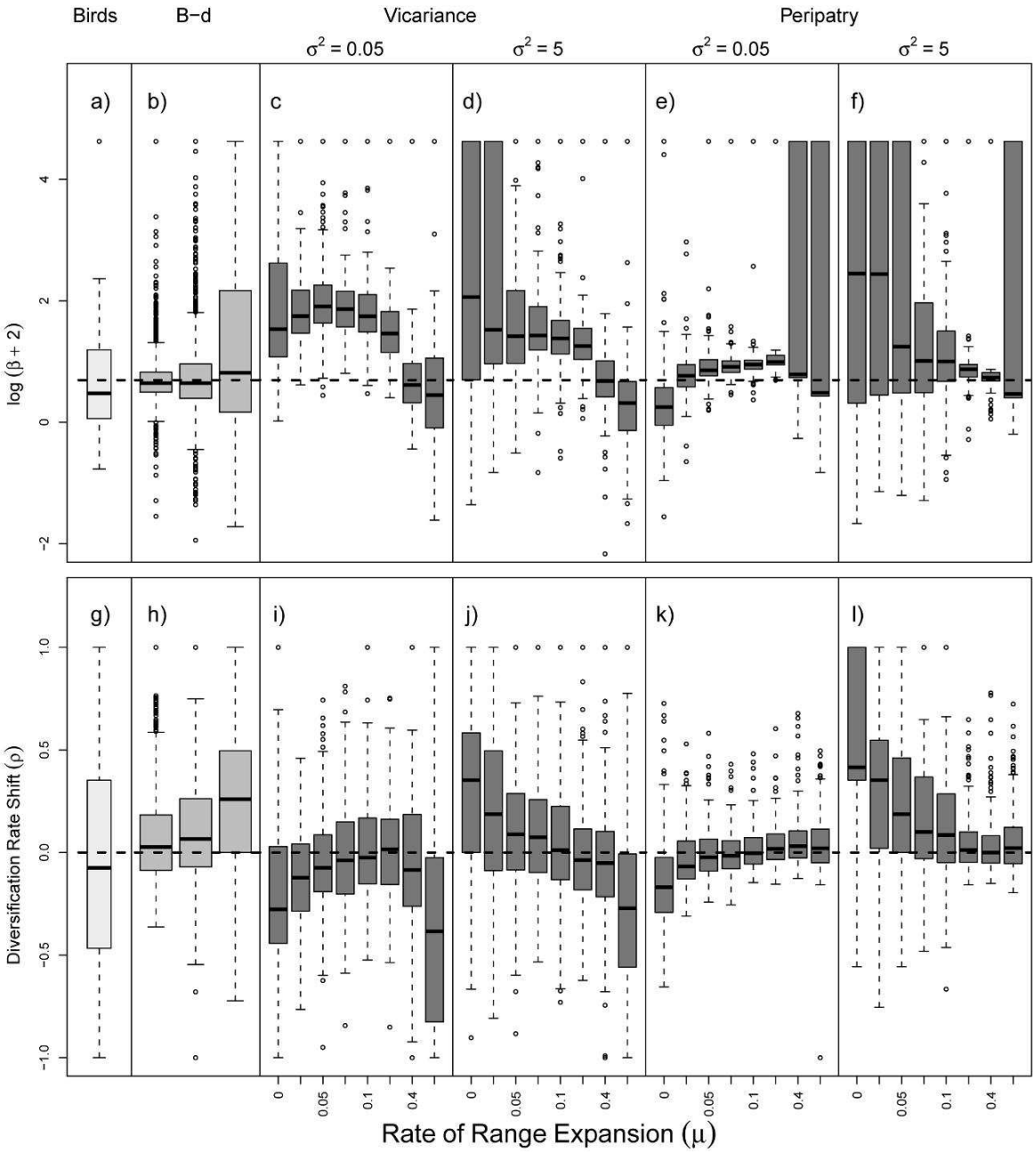


Figure 2.5. Comparisons of tree imbalance (log transformed β splitting parameter + 2) and shifts in diversification rate (ρ) for bird genera (a,g), birth-death models (B-d) (b,h) and geographical models (c-f, i-l), showing the expectation under a constant-rate pure-birth model (dashed lines). Birth-death models (b,h) used a constant speciation rate (b=0.2) and varying levels of extinction (left to right, d= 0, 0.05 and 0.2).

2.4.2 Phylogenetic tree imbalance and the distribution of range sizes

Under most combinations of speciation mode and range dynamics the model predicts positively skewed range size frequency distributions (RSFD's) (Figure 2.4l-o), mirroring the strong skew in range sizes observed across bird genera (median g = 1.43) (Figure 2.4k). In the vicariance model this occurs due to the tendency for barriers to result in the asymmetric division of species' ranges (Figure 2.4l). The peripatry model produces particularly strongly skewed RSFD's due to the persistence of a few species with large geographic ranges and production of many small peripheral isolates (Figure 2.4n). The closest approximation to the skew observed in the RSFD's of bird genera, occurs when speciation is by vicariance and rates of range expansion are low (μ=0.05), a result that is insensitive to the degree of stochasticity in range movement. Realistic levels of skewness also occur in the peripatric model, but the conditions are more restrictive, requiring both low rates of range expansion (μ=0.05) and highly stochastic range movement (σ^2=5).

The differences in range sizes amongst species lead to variation across lineages in the probability of diversification. Under a peripatric model, with no tendency for ranges to expand (μ=0), highly unbalanced trees are produced (median β = -0.71) (Figure 2.5e) compared to that expected under a birth-death model (Figure 2.5b). Indeed, levels of imbalance are comparable to that observed in real bird trees (median β = -0.51, Figure 2.5a). This is because the production of small peripheral isolates does not reduce the range size of the ancestral lineage, which is able to continue speciating at the same rate. In contrast, despite variation in range size amongst lineages, trees produced under a vicariance model are highly balanced (median β = 1.8) (Figure 2.5c,d) compared with observed clades of birds (Figure 2.5a) and the birth-death model (Figure 2.5b). This occurs because, although range sizes are

skewed, lineages that experience rapid diversification also exhibit a reduction in range size, reducing opportunities for further cladogenesis. An additional factor leading to more balanced tree topologies in the vicariance models is the tendency for barriers to simultaneously bisect multiple species' ranges.

The dynamics of ranges following speciation has complex effects on tree imbalance and range size distributions. When rates of range movement are low (σ^2=0.05), but ranges have a tendency to expand, this leads to more balanced trees because even species with initially restricted distributions are likely to speciate (Figure 2.5c,e). However, when rates of range movement are high (σ^2=5) the effect of range expansion on tree balance is reversed. This is because when there is no tendency for range expansion, species with small ranges rapidly go extinct leading to less skewed RSFD's and more balanced trees (Figure 2.5d,f). In contrast, when ranges have a tendency to expand, species with small ranges are saved from extinction leading to more positively skewed RSFD's (Figure 2.4m,o) and more unbalanced trees (Figure 2.5d,f), converging on the expectation of the equal rates birth-death model (median = 0.19) (Figure 2.5b).

2.4.3 Phylogenetic signal in range size

Within bird genera, range size tends to exhibit a low phylogenetic signal ($\lambda < 0.2$ in 29 of 41 cases) (Figure 2.4p). Similarly low levels of λ are obtained under both the vicariance and peripatric model (Figure 2.4q-t). A weak phylogenetic signal is found regardless of the rate at which ranges fluctuate through time, occurring under both highly volatile and highly stable conditions (Figure 2.4q-t). The main cause of low λ estimates is therefore not the rate at which ranges are stochastically changing in size through time (simulations show that the product of

two Brownian processes on its own leads to high estimates of λ, similar to a Brownian process). Rather, the weak phylogenetic signal arises because of the highly non-Brownian way ranges are "inherited" during speciation under the vicariance and peripatry models. High rates of range expansion lead to higher values of λ, by increasing the variance of range sizes amongst the ancestors of present-day species (Figure 2.4q-r). Eventually, however, under very high rates of expansion, species tend to fill the domain and the phylogenetic signal subsequently declines (Figure 2.4q-r).

2.5 Discussion

2.5.1 The geography of diversification

A fundamental assumption of the birth-death model is that the probabilities of speciation and extinction are independent of the history of cladogenesis (Losos & Adler 1995). However, the bifurcation of a lineage in a phylogenetic tree will usually arise because of the splitting of its geographic range in space (Coyne & Orr 2004). Newly formed sister lineages will, therefore, occupy only a fraction of the parental range, and may differ markedly in size depending on the geometry of range division and mode of geographic isolation (Anderson & Evensen 1978; Barraclough & Vogler 2000; Waldron 2007). Consequently, if the probabilities of speciation and extinction rates are dependent on the geographical extent of a species (Rosenzweig 1975), variation in the rates of diversification through time and amongst lineages are expected (Losos & Adler 1995). Here I show that considering the geography of speciation and extinction has a profound influence on the phylogenetic patterns of diversification expected in the absence of ecology.

Highly unbalanced trees and strong temporal slowdowns in diversification are often observed in real phylogenies but do not arise under the standard birth-death model, leading to the widespread perception that species biological traits and ecological interactions underlie the dynamics of species radiations (Mooers & Heard 1997; Phillimore & Price 2008; Slowinski & Guyer 1993; Weir 2006). However, the models show that these patterns can also arise simply because of the feedback on speciation and extinction rates imposed by the division of geographic ranges during speciation. These results suggest that even for groups representing classic cases of adaptive radiations (Losos et al. 1998; Schluter 2009), we should not discount the possibility that the rate of diversification has been limited by the geographical opportunity for isolate formation and range expansion rather than the availability of unutilised niche space (Rundell & Price 2009) (e.g. many of the Greater Antillean Anolis sister species are in fact allospecies found on separate mountains on a single island (Losos & Parent 2009)). This neutral perspective does not preclude the role of niche expansion and adaptation in initiating species radiations (Nee et al. 1992). Indeed, if range sizes decline due to speciation then rare events which promote range expansion, such as key innovations, may be essential in renewing the process of diversification.

2.5.2 The geographical mode of speciation

The way in which geographical isolation occurs in the model, has a strong effect on the dynamics of cladogenesis. Under a vicariance scenario, speciation leads to successive reductions in range size and a declining rate of diversification, particularly in those branches where speciation has been most rampant. The result is a strong temporal decline in the diversification rate and highly balanced topologies. When speciation occurs via dispersal, the

production of small peripheral isolates also leads to a decline in the average range size and thus slowdown in speciation rate. However, in contrast to the vicariance model, the range size of one of the daughter lineages is not eroded by the process of speciation. Lineages that have been prolific speciators will therefore continue to be so, producing extremely unbalanced tree topologies. A similar result is obtained for Hubbell's point mutation speciation model since here most newly formed species are extremely rare i.e. singletons (Mooers et al. 2007).

Variation in range shape is also an important determinant of speciation in the model. For a given range size, linear distributions are more prone to bisection by geographic barriers (Graves 1988; Rosenzweig 1978) and more likely to give rise to dispersal events. Mathematical models of the genetic basis of speciation also predict that one-dimensional geographic distributions should lead to higher speciation rates because of lower connectivity and gene flow between populations (Gavrilets 2004) (see Chapter 5). The dynamic relationship between range shape and diversification rate in the models is similar to that of range size: in the vicariance model the random division of a linear range tends to give rise to daughters with more compact distributions, further confounding the potential for future speciation, whereas no such trend occurs in the dispersal model.

2.5.3 Range evolution and the role of geographical speciation

For continental radiations, it has been argued that the most likely way in which niche saturation impinges on diversification rates is through a heightening of competition and the progressive limits to range expansion and thus opportunities for speciation (Phillimore & Price 2009; Price 2008; Rosenzweig 1975). Such a model implies that in the absence of competition, ranges would rapidly expand following speciation. Indeed, when ranges have a strong

tendency to expand, rates of diversification are more constant through time. However, species' distributions, particularly at large spatial scales (Russell et al. 2006), are often thought to be set for reasons other than competition, including; physiological limits, (Root 1988a) habitat structure (Holt et al. 2005) and dispersal barriers (Goldberg & Lande 2007). These limits may be stable over evolutionary time due to a lack of genetic variability (Kellermann et al. 2009), developmental constraints or genetic swamping preventing adaptation (Kirkpatrick & Barton 1997). While species may be able to adapt and subsequently expand their distributions, the timescales for niche evolution may be comparable to that typically assumed for speciation (Wiens & Donoghue 2004). A signal of slowdowns in the diversification rates of large clades with small geographic ranges is therefore, by itself, insufficient evidence for competition in limiting range expansion and speciation. One way in which the role of competition in generating slowdowns could be tested, would be to modify the models developed here to prevent sympatry amongst lineages that have recently split/arisen.

Previous studies have shown that when range dynamics are highly volatile the signal of speciation in the distributions of extant species is rapidly eroded, making the geographical mode of speciation difficult to detect (Barraclough & Vogler 2000; Losos & Glor 2003; Phillimore et al. 2008). Here I show that when range volatility is high, the reconstructed patterns of diversification are also drastically altered. Only under conditions of relatively stable range sizes should we expect strong slowdowns in diversification rate and high tree imbalance. Changes in species' distributions can be highly volatile, occurring over short timescales compared to that required for speciation (Davis & Shaw 2001; Lessa et al. 2003). However, the extent to which such high rates of range evolution are typical of clades in general is unclear. Phylogenetic signal in range size is typically weak, with most variation occurring amongst low

taxonomic levels (Waldron 2007), and this is often interpreted as evidence that range size is highly labile (Freckleton & Jetz 2009; Gaston 1998). However, the models show that even when range sizes vary little through time according to a random-walk process that on its own leads to range size having a strong phylogenetic signal, the apportioning of geographic ranges during speciation, and the corresponding substantial departure from a Brownian model of evolution, ensures that the phylogenetic signal is low. A faster rate of range evolution on its own leads to similarly high estimates of phylogenetic signal, as is the case with a Brownian model (Revell et al. 2008). However, as faster range evolution leads to a greater frequency of extinctions this censoring may dampen phylogenetic signal in addition to the effect of the speciation process. Taken together, a perhaps surprising finding of this study is that low phylogenetic signal does not therefore provide strong evidence for the lability of geographic ranges.

2.5.4 Incorporating geography into models of diversification

In the model developed here, altering the range dynamics and mode of speciation gives rise to wide variation in the temporal dynamics and shape of phylogenetic trees. As a result, the appropriate null expectation of imbalance and slowdowns for a clade will differ depending on the conditions characterising its evolution. For instance, if vicariance has been the predominant mode of speciation within a clade then a highly unbalanced topology would be even less explicable by a random process than comparison to a birth-death model would suggest. Conversely, if most speciation has occurred via peripatry then high imbalance would be expected by chance alone and would not require explanations based on ecological differences amongst species. Moreover, the models show that a pattern of equal and constant rates of

diversification is only expected under particular scenarios of range evolution and speciation mode; namely when rates of range expansion and dynamism are high and speciation occurs by peripatry. When these conditions do not accurately characterise the history of a clade the use of an equal and constant rates birth-death model would therefore be inappropriate.

A number of studies have examined the effects of altering the assumptions underlying the birth-death model on patterns of phylogenetic tree imbalance. For example, Chan and Moore (1999) showed that when speciation results in a decline in the probability of diversification for both daughter lineages, as in the vicariance model, this leads to more balanced trees. When only one of the daughter lineages exhibits a reduction in speciation rate, as in the dispersal model, more unbalanced trees are produced (Chan & Moore 1999; Rogers 1996). The causes of such refractory periods have generally been cast in a geographic context e.g. the time required for ranges to expand following speciation (Losos & Adler 1995). Heard (1996) and Rogers (1996) found that when per lineage speciation rates evolved according to either a gradual or punctuated model, the trees produced were more unbalanced; a scenario approximating the peripatric model of speciation that I investigated. By simulating the underlying dynamics of species' ranges and the process of geographic isolation the model generalises and extends these findings. For instance, while the impact on speciation of a short refractory period is equivalent to a scenario in which ranges have a strong tendency to expand (Losos & Adler 1995), range expansion also reduces the extinction rate with complex effects on the distribution of geographic range sizes and subsequent dynamics of diversification.

Nevertheless, the model makes a number of simplifications which future studies should address. Vicariance was simulated using a simple model of linear barrier formation but other ways of modelling range division may lead to differences in how the probability of

speciation scales with range size and in the resulting asymmetry in daughter species' range sizes (Rosenzweig 1978; Waldron 2007). In the absence of empirical information on the geographic barriers found in nature I chose arbitrary barrier length distributions, with the barriers dropped at random onto the domain, while in reality barriers may be more frequent at continental margins (e.g. mountain ranges and rivers). A further simplification in the model was the assumption that species' range margins shift independently through time. In particular biogeographic settings, directions of range expansion, and thus patterns of geographic range size and shape, may be more constrained (see Chapter 3). Moreover, if changes in the position of range boundaries are correlated, then large shifts in species' distributions may occur without substantial changes in geographic range size (e.g. parallel shifts in the northern and southern boundary of a range in response to climate change). Such a scenario may extend the breadth of parameter space under which a geographical model can account for observed patterns of diversification.

The imbalance and temporal dynamics of the bird phylogenies I examined seem to be best explained by the dispersal model with little post-speciation changes in geographic range size. This model, however, predicts unrealistically high levels of skew in the distribution of range sizes, suggesting that the patterns in clade shape across bird genera are unlikely to be explained by a single region of the parameter space I explored. This is perhaps not unexpected given the disparate histories of real clades, including their ancestral range sizes, geographical locations and opportunities for range expansion (Ricklefs 2006a; Weir et al. 2009). Moreover I did not explore the more realistic scenario where vicariance and dispersal each contribute to the origin of new species. In the future, it may be possible to estimate the combination of geographic parameters that are most likely to have given rise to the observed phylogenetic and

distribution patterns in a likelihood framework or using approximate Bayesian techniques. For instance, clades diversifying predominantly by peripatry may be characterised by more asymmetric ranges and shorter lived species that those produced by vicariance (see Chapter 4).

2.6 Conclusion

Although a model of equal rates amongst species and constant rates through time is regarded as the most parsimonious model of cladogenesis (Nee 2006), from a geographic perspective, such a scenario requires that the range sizes of daughter species are similar to both that of the parent and to each other, implying either that range size is strongly heritable (Jablonski 1987) or that the geographical signal of lineage splitting is completely scrambled by post-speciation range evolution. Accordingly, in the simulations, the closest approximation to a birth-death model is reached under a peripatric model of speciation with high rates of range growth and highly volatile fluctuations in range boundaries. When viewed in a geographical context then, the birth-death model represents only a small region of parameter space, with the occurrence of equal and constant rates requiring a rather restrictive set of biological conditions to be fulfilled.

Chapter 3

The environmental limits to geographic range expansion in birds

3.1 Abstract

The environmental factors limiting species' ranges across broad geographic and taxonomic scales are central to questions regarding the geographic variation in biodiversity and impacts of environmental change. However, our understanding remains relatively limited owing to the small-scale, correlative nature of most previous analyses. Here I provide a global test of the environmental determinants of range limits in birds, by using both stochastic and environmentally deterministic models of range expansion to simulate spatial patterns in the shape of species' distributions. I show that spatial variation in range shape can be well explained by the action of a few key climatic variables in limiting range expansion. The factors constraining range expansion differ between biogeographic realms and between widespread and rare species. Although temperature was the principal climatic determinant of range shape at a global scale its effects were driven primarily by widespread species, with the ranges of rare taxa better predicted by gradients in precipitation or topography. Simulation of random range expansion showed that the patterns in range shape cannot be explained by random processes. Taken together, these findings helps resolve long running debates regarding

the role of environmentally deterministic and stochastic processes in structuring biodiversity and extends our understanding of the factors limiting species' ranges and the response of broad scale biodiversity patterns to environmental change.

3.2 Introduction

Understanding the determinants of species' ranges lies at the heart of explaining the uneven distribution of biodiversity over the Earths surface (Janzen 1967; Terborgh 1973). Climate has long been regarded as exerting a primary control over terrestrial species' ranges (Grinnell 1914; Merriam 1894), and many studies have since documented strong associations between individual species' range limits and a multitude of climatic indices (Gaston 2003; Sexton et al. 2009). Indeed, it is because of this paradigm that species are expected to shift their distributions under climate change. Yet, despite this pivotal role and decades of interest (Grinnell 1914; MacArthur 1972; Merriam 1894), our understanding of the identity and explanatory power of the environmental factors constraining geographic ranges across broad geographic and taxonomic scales remains relatively poor (Brown et al. 1996; Gaston 2003; Gaston 2009; Parmesan et al. 2005).

A key reason for the lack of agreement regarding the factors limiting geographical ranges is that the majority of studies to date have been limited both in the number of species analysed and their spatial extent (Brown et al. 1996; Gaston 2003). Much of our knowledge still consists of what Robert MacArthur (1972, pg.127) termed "catalogs of special cases". As a result, a plethora of potential factors have been identified, but these are often species - or location-specific (Brown et al. 1996). Very few attempts have been

made to investigate the co-occurrence of range edges across multiple species and at continental scales (McInnes et al. 2009; Root 1988a; Root 1988b). In this study, I aim to overcome these limitations by examining the environmental determinants of the geographic ranges of an entire class of organisms, Aves. To do this, I take a relatively unusual approach, by analysing the shapes of species' ranges (Rapoport 1982).

The climatic niche of a species encompasses the conditions under which its individuals are able to survive and reproduce (Hutchinson 1957; Pulliam 2000). The distribution of a species can be conceptualised as the projection of these conditions onto geographic space (Colwell & Rangel 2009). Spatial variation in the environmental factors defining a species' niche, and thus constraining range expansion, should therefore be reflected in the size and shape of the distribution (Grinnell 1917; Rapoport 1982). While the causes of geographic range size have received much attention (Gaston 2003), interpretations of these patterns are complicated by factors such as differences in niche breadth and dispersal ability (Bohning-Gaese et al. 2006). In contrast, for a given range size, variation in range shape should primarily reflect the configuration of the climatic gradients responsible for limiting range expansion (Brown & Maurer 1989; Rapoport 1982; Ruggiero 2001; Ruggiero et al. 1998).

To investigate the environmental factors limiting range expansion, I used a spreading dye algorithm (Jetz & Rahbek 2001; Storch et al. 2006) to reconstruct the configuration of geographic ranges expected when ranges are limited by a variety of environmental parameters. I then compared the spatial variation in the shape of these simulated distributions to that observed for real species' ranges. I also investigate the idea

that either the patterns in range shape, or the associations with climatic indices, could have arisen by chance (Beale et al. 2008; Root 1988a; Root 1988b). Neutral models of species' ranges governed only by random local dispersal and stochastic extinction (Hubbell 2001) predict that distributions would be approximately circular in shape (Skellam 1951). For terrestrial species with large geographic ranges, however, the boundaries of the continents may constrain their distributions (Colwell & Lees 2000; Jetz & Rahbek 2001) giving rise to irregularly shaped ranges in the absence of environmental gradients (Sandel 2009). Testing whether species' ranges depart from random models is therefore essential to avoid attributing patterns to potentially spurious deterministic causes (Peterson et al. 2009; Root 1988b). Although null models have held a central position in debates regarding the relative roles of stochastic and deterministic processes in species richness gradients (Jetz & Rahbek 2001; Rahbek et al. 2007; Storch et al. 2006), they have yet to be applied to the study of the species' ranges that underlie these gradients (Gotelli et al. 2009; Peterson et al. 2009). I therefore ask, to what extent can the associations I find between the environment and the shape of the species range be explained by null models of random range expansion?

Here, I examine the environmental factors limiting species' ranges in birds. I address this question both at a global scale and within individual biogeographic realms and range size quartiles. I attempt to avoid the criticisms levelled at statistical models of geographic ranges by using a process-based model of range expansion to examine the link between species' ranges and the environment. This approach also allows me to address the long running debate regarding the role of stochastic and deterministic processes in structuring large scale patterns of biodiversity. Finally, throughout the

analysis I use two different methods to quantify variation in range shape to ensure that the results are not artifacts of a particular method.

3.3 Methods

3.3.1 Data

I used a global database on the breeding extent of all extant terrestrial birds (9,626 species) that has been the focus of a number of studies of species richness and range size (Davies et al. 2007; Orme et al. 2005; Orme et al. 2006; Storch et al. 2006). The analysis of range shape involved the use of cell based simulations (e.g. Jetz & Rahbek 2001; Storch et al. 2006), and so the vector range maps were converted into a gridded format, using the equal-area Behrman projection with a cell size of 96.486 km, equal to 1° longitude at 30° latitude (Orme et al. 2005). A smaller grain size would permit analysis of range shapes at a finer resolution and reduce the overestimation in range size, particularly for species with linear distributions (Rahbek 2005). However, these concerns need to be weighed both against computational tractability of conducting simulations at this scale, and the accuracy of global species' ranges (Hurlbert & Jetz 2007). A scale of around 1° is generally considered to be the finest resolution appropriate for global scale distribution data (Hurlbert & Jetz 2007). Using an equal area projection was necessary because of the need to conserve range sizes in the cellular based simulations (Storch et al. 2006). Although the shapes and distances between cells in the grid are not constant, this distortion is only marked at very high latitudes where few species live (see Figure S1 in Gaston et al. 2007). I was interested in the factors controlling ranges on large landmasses, so I only included those species, or portions of species' ranges, that occurred on

continents (excluding Antarctica, where few species live and where environmental data is lacking). I also excluded species with ranges consisting solely of fragments smaller than three cells because these ranges will have a constant shape and are thus uninformative (Appendix 2 Figure S1). This resulted in the inclusion of 7,484 species in the analysis.

3.3.2 Quantifying range shape

Previous studies investigating patterns in range shape have employed simple shape measures, such as N-S and E-W extent (Brown & Maurer 1989; Sandel 2009), but these fail to capture much of the detail in range configuration. The perimeter to area ratio has also been used to measure the shape of isodensity maps (Rapoport 1982; Ruggiero 2001; Ruggiero et al. 1998), a rough proxy for spatial patterns in range shape. Shape indices incorporating the perimeter are, however, highly sensitive to irregularities in the range boundary (Brown et al. 1996; Maceachren 1985; McGarigal & Marks 1995). As a result, indices based on maximum linear (l) and areal dimensions (a), are known to be more appropriate for quantifying shape circularity (Maceachren 1985).

To ensure that the results were not dependent on the index used to quantify range shape I used two alternative methods to calculate the shape of each species' range (R_s). The first method, that I term the Range Linearity Index, is based on the area (a) and maximum linear dimension (l) according to the following formula; $R_s = l^2/a$. This measure is equivalent to the long axis to width ratio, with higher values indicating more elongated geometries (Graves 1988; Niemi et al. 1990). I calculated the long axis as the longest path distance through the range (see Appendix 2 'Range linearity index' and Figure S1). The second method used to quantify range shape, which I refer to as Maurer's

Shape Index (Maurer 1994), uses the variance-covariance matrix of distances between occupied cells to indentify the two principal shape axes. The index is then calculated as the scaled difference in the length of these two axes (see Appendix 2 'Maurer's shape index'). For both indices, the shape of ranges consisting of multiple fragments were determined by first calculating the shape for each fragment separately and then calculating an area-weighted shape value across fragments (Appendix 2 Figure S1).

I selected these two indices of range shape because their differing assumptions make them complementary in their advantages and limitations. Maurer's Shape Index has the advantage of incorporating the distances between all occupied cells when calculating the shapes primary axes, but assumes these axes to be straight and orthogonal to one another (Maurer 1994). By contrast, the Range Linearity Index restricts measurement of the range long axis between the two most isolated occupied cells, but has the advantages of using a more accurate method to calculate distance across the range (path distance) and does not assume the shapes axes to be orthogonal. In order to minimise redundancy, I present the detailed results for only the Range Linearity Index in the main paper and present the results based on Maurer's Index in the supplementary material (see Appendix 2 Table S1, S2, S3). Throughout the text, however, I highlight any cases where the methods provide qualitatively different results with respect to the main conclusions.

3.3.3 Simulating range shape

To simulate the patterns of range shape expected under a model of random range dynamics limited only by the continental boundaries, I employed a modified version of the spreading dye algorithm (Jetz & Rahbek 2001; Storch et al. 2006). Species were

seeded from a single cell on the continental domain and then allowed to randomly spread into adjacent unoccupied cells until their observed range size is reached. In order to maintain range cohesiveness I only allowed expansion to occur into cells sharing an edge with those already occupied. I also imposed the following additional constraints on the simulations. First, I preserved the approximate positions of species in space by selecting the starting cell at random from within the observed species' range. Studies investigating null models of species richness have randomised the position of geographic ranges (Jetz & Rahbek 2001; Rahbek et al. 2007; Storch et al. 2006), but here I was interested in the determinants of species' range boundaries, given the known geographical position of their distributions. Second, I preserved the observed number and size of fragments comprising a species' range, by seeding and simulating each fragment simultaneously. This avoided the bias toward more compact ranges arising through simulation of a single, and thereby necessarily larger, aggregated range. It also bypassed the need to simulate the process of fragmentation, which would have required additional assumptions (Rangel et al. 2007). Fragments were prevented from merging by removing candidate cells already occupied or sharing an edge with another fragment. If envelopment by other fragments prevented further spread the simulation for that species was re-run.

The simulations described above were modified in order to assess the role of environmental gradients commonly invoked as correlates of range boundaries (Gaston 2003; Rapoport 1982; Root 1988a; Root 1988b). These were; mean annual temperature (New et al. 2002), mean annual precipitation (New et al. 2002) and net primary productivity (NPP) (Imhoff et al. 2004). I also investigated the effects of mean elevation (USGS EROS Data Center available at http://eros.usgs.gov/products/

elevation/gtopo30.php). I included elevation because although elevation *per se* is unlikely to influence species' ranges, it represents a surrogate variable of small scale environmental variability consistently used in broad scale studies of bird species richness and range size (Davies et al. 2007; Graves & Rahbek 2005; Hawkins & Diniz-Filho 2006; Jetz & Rahbek 2002; Rahbek et al. 2007; Rahbek & Graves 2001). All environmental variables were resampled using the equal-area Behrman projection, with a cell size of 96.486 km to match the resolution of the species grid.

I rescaled all the environmental variables to between zero and one, thus assuming equivalence in the effects of a given proportional change on colonisation probability (Rangel et al. 2007). For each variable, the average observed value within each range fragment (Rangel & Diniz-Filho 2005) was assigned as the environmental optimum for that fragment. The starting and subsequent cells for range spread were then chosen with a probability based on the distance from this optimum (Rangel & Diniz-Filho 2005). I used a simple exponential decay model of cell suitability with increasing absolute difference (d) of the cell value from the fragment optimum: $(d+1)^{-s}$. The exponent *s* allows variation of the degree of environmental determinism in cell selection from completely random (s=0), as in the null model above, to highly deterministic. I used an *s* value of 30, representing strong environmental determinism with a halving of relative suitability for cells separated by 0.023 scaled units. The relative probability of colonisation for each cell was calculated by dividing the suitability score for each cell by the cumulative suitability across all candidates. I also examined the interaction between temperature and precipitation by setting the probability of colonising a cell as a product of the individual probabilities of each environmental variable (Rangel et al. 2007). I did not explore

interactions involving NPP or elevation because these are either partially derived from or strongly collinear with climatic variables. For each model, I simulated all species' ranges and measured their shapes as described. I then calculated the median range shape within each cell and used the average of these from across 100 such simulations in the analysis.

3.3.4 Statistical analysis

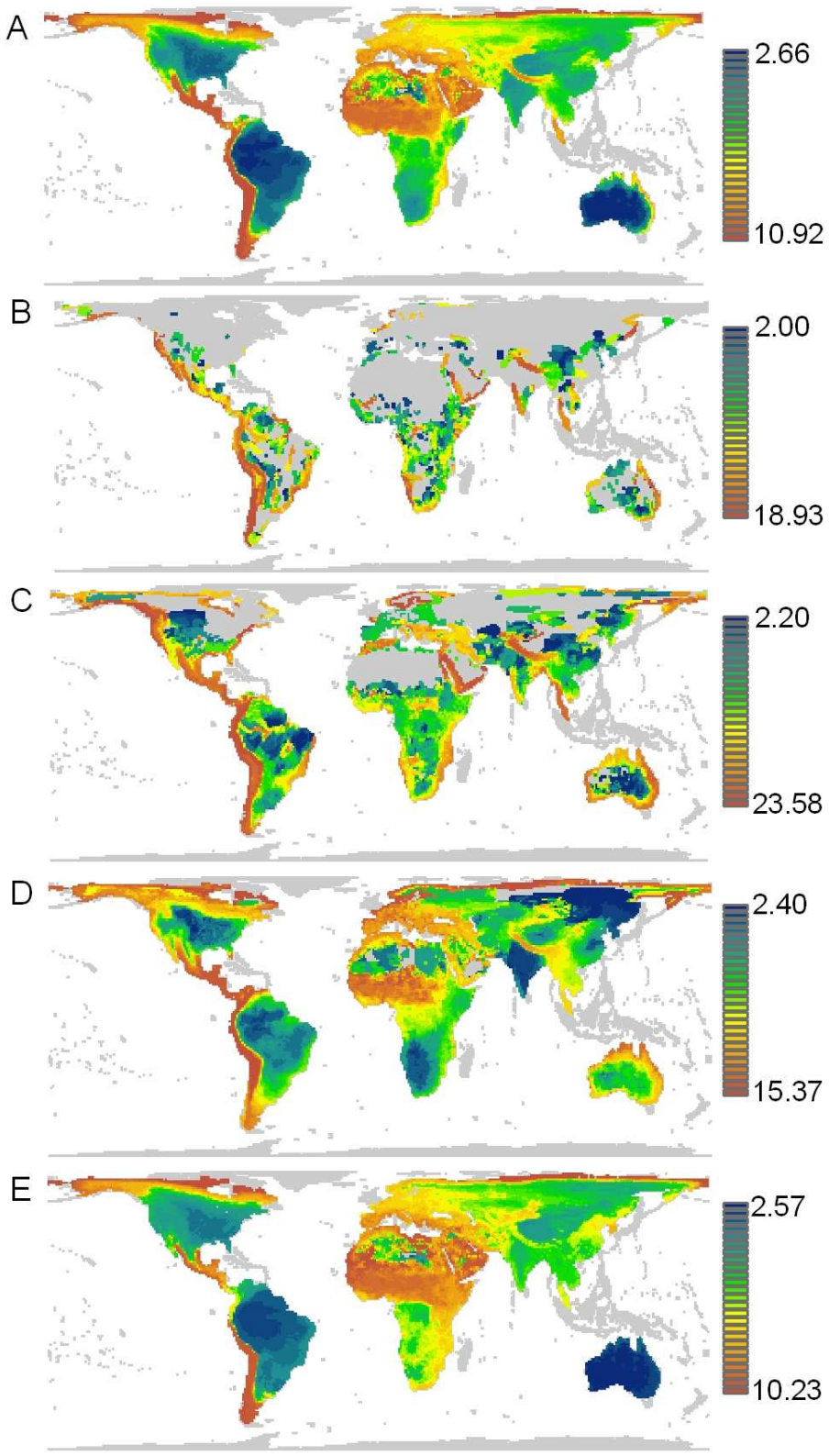
I investigated the association between observed and simulated patterns in range shape using standard ordinary least squares (OLS) regression. I used the natural logarithm of median range shape within each cell in the analysis to improve normality in the model residuals. As an additional measure of model performance I also used "unity line" (UL) regressions, in which I compared the simulated shape values to a line with a slope of one and intercept of zero, which would indicate a perfect correspondence between observed and simulated range shape (Romdal et al. 2005). For the global analysis, I accounted for spatial autocorrelation in model residuals using simultaneous autoregressive models (SAR) (Kissling & Carl 2008), fitted using the R package spdep (http://cran.r-project.org/). I implemented the spatial error model category because this has been shown to produce both the most reliable parameter estimates and adequate control of autocorrelation (Kissling & Carl 2008). The variables were rescaled and centred on zero before fitting the models and the spatial structure was specified as the eight nearest neighbours to each cell. I assessed the relative explanatory power of the SAR models using Akaike's Information Criterion.

3.4 Results

3.4.1 Global patterns in range shape

The shapes of avian geographic ranges exhibit striking geographical patterns (Figure 3.1a), varying from regions where ranges are predominantly circular (e.g., the Amazon and Eastern North America) to regions characterised by highly elongated distributions (e.g., Central American Isthmus and high Northern Latitudes). These overall patterns were principally driven by widespread species (3rd and 4th quartile) (Figure 3.1 d-e). When only restricted-range taxa are considered (1st and 2nd quartile) the most linear distributions are found along coastlines and low latitude mountain chains (e.g. Andes and Himalayas). Restricted-range species occurring within the lowlands of continental interiors have more circular distributions, with the exception of the linear ranges along some major rivers (e.g. the Amazon).

Figure 3.1. On the following page. Spatial patterns in observed avian geographic range shape for, (a) all species and for each range size quartile (b-e) (first, second, third, fourth) using the Range Linearity Index. Areas in red indicate more linear distributions, while areas in blue indicate more circular ranges and are plotted in quantiles with 25 levels. Grey cells indicate land area not included in study. Maps are plotted in an equal-area Behrman projection.


A
2.66
10.92
B
2.00
18.93
C
2.20
23.58
D
2.40
15.37
E
2.57
10.23

The extreme linearity of bird species' ranges in the Andes has previously been noted (Graves 1988; Ruggiero 2001) and it is clear that even at the relatively coarse scale of analysis used here, the Andes are exceptional in the preponderance of species with linear distributions. The spatial patterns according to Maurer's Index were broadly similar to that of the Range Linearity Index (all species model, OLS r^2=0.49) but the two methods also captured different aspects of range shape. These differences were most apparent for species within the 4th range size quartile, with Maurer's Index highlighting the elongation of ranges at Northern high latitudes and down weighting the variation in other regions compared to the Range Linearity Index (Appendix 2 Figure S2).

3.4.2 Random models

The simulations showed that, even when range spread occurs at random, this does not lead to uniform patterns of range shape (Figure 3.2a). Instead, the limits imposed by the continental domain funnel ranges to spread in certain directions (Sandel 2009), resulting in elongated distributions in narrow peninsulas and isthmi (e.g., Malaysian penninsula), with the continental interiors characterised by more circular ranges (e.g., Amazon basin). Furthermore, when ranges are simulated by the sequential addition of cells then, under the law of large numbers, widespread species tend towards circularity while restricted distributions exhibit both circular and elongated geometries. Consequently, regions of high endemicity (e.g., the Andes, Graves & Rahbek 2005; Orme et al. 2006) are more likely, simply by chance, to be characterised by elongated ranges.

The patterns predicted by the null model were significantly positively associated with that of the actual species' ranges (Table 3.1). In fact, although explanatory power

was relatively low (OLS r^2=0.16; Table 3.1), both the null OLS and SAR models explained a greater variance in range shape than did some of the environmental parameters. However, although the null model explained more variation, it was substantially displaced from the expected unity line relationship (UL r^2=0.01) (Table 3.1). Indeed, even where the continental domain is relatively narrow, and the effects of geometric constraints likely to be most pronounced, the ranges are too circular with points falling far above the line of unity (Figure 3.3a). As expected, the explanatory power of the null model varied between realms (Figure 3.4a; Table 3.2) and increased with range size (Figure 3.4b; Table 3.3). However, even for the largest range size quartile, only 18.5% of the spatial variance in range shape is explained by a null model and there is an extremely poor fit to a unity line (Table 3.3). All of these findings remained qualitatively unchanged when I used the alternative method for quantifying variation in range shape (Appendix 2 Table S1; Table S2; Table S3).

3.4.3 Global environmental models

The models of range spread driven by environmental gradients each resulted in unique patterns in the shapes of species' ranges (Figure 3.2b-f). Elevation (OLS r^2=0.25, UL r^2= 0.07) and temperature (OLS r^2=0.23, UL r^2= 0.07) were the strongest environmental predictors at a global scale, with precipitation (OLS r^2=0.15, UL r^2=0.03) and net primary productivity (NPP) (OLS r^2=0.13, UL r^2=0.03) accounting for less variation (Figure 3.3b-e and Table 3.1). In this case, using Maurer's Shape Index modified the relative explanatory power of the models, increasing the fit of the null and temperature based

model and decreasing the fit of the models based on precipitation, NPP and elevation (Appendix 2 Table S1).

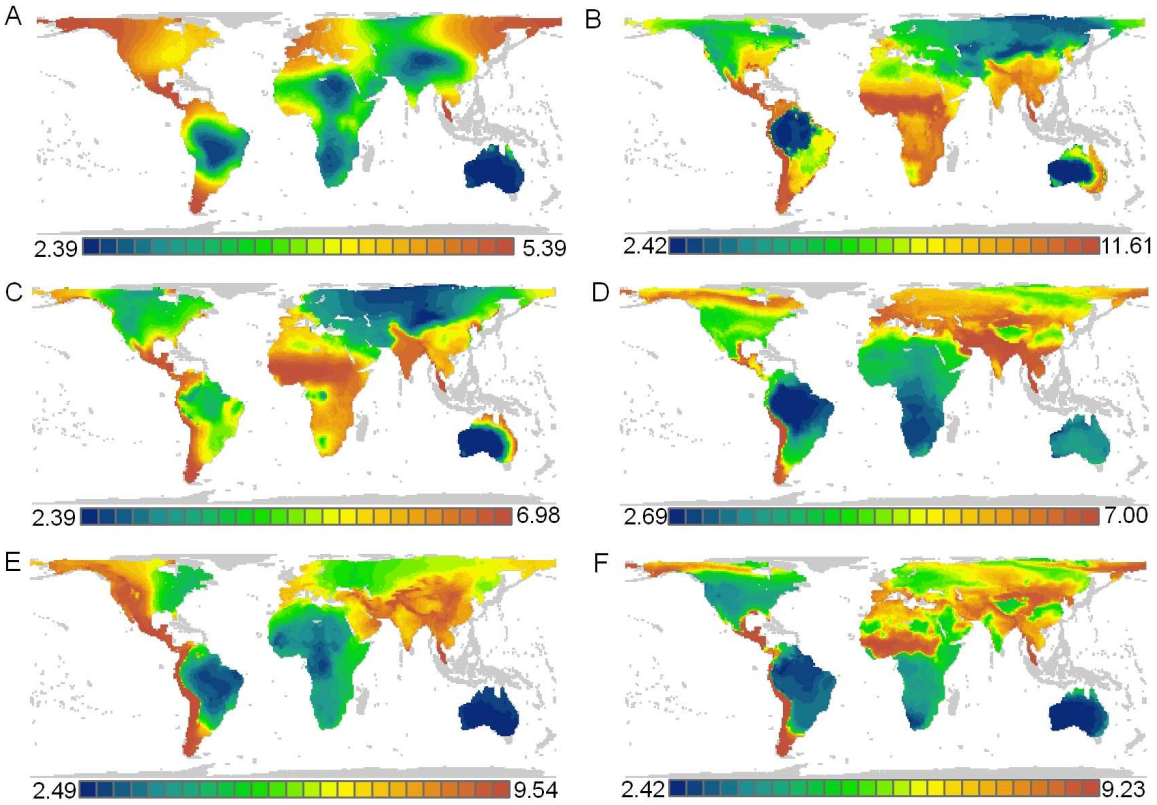


Figure 3.2. Spatial patterns in range shape predicted by (a) the null model of range expansion occurring in the absence of environmental gradients and (b-f) the deterministic models limited by various environmental parameters; (b) Net Primary Productivity, (c) precipitation, (d) temperature, (e) elevation and (f) precipitation * temperature. Cell values represent the average across 100 simulations and are plotted in quantiles with 25 levels. Note the differences in scale between maps.

Predictor	Non-Spatial Models					Spatial Models		
	OLS				UL	SAR		
	Intercept	Slope	r^2	AIC[a]	r^2	Intercept	Slope	AIC
Null	0.79	0.79	0.16	39252	0.01	0.02	0.4	7192.6
NPP	1.25	0.27	0.13	39891	0.03	0.02	0.24	7993.2
Precipitation	1.01	0.49	0.15	39440	0.03	0.01	0.32	7564.9
Temperature	0.99	0.47	0.23	38082	0.07	0.02	0.44	6629.7
Elevation	1.02	0.45	0.25	37632	0.07	0.02	0.45	6184.5
TemperatureXPrecipitation	0.35	0.9	0.59	28827	0.25	0.01	0.61	3492.4

Table 3.1. Global models for spatial patterns in geographic range shape. Results are presented for both the non-spatial and spatial analysis of the observed patterns in range shape against those predicted by the simulations. Abbreviations are as follows; Ordinary Least Squares (OLS), Unity Line (UL), Simultaneous Autoregressive (SAR) and Akaike's information criterion (AIC). Raw data are the median values of range shape within each cell. The data was log_e transformed prior to analysis. The environmental predictors refer to those variables used to limit range expansion in the simulations. Interactions between variables indicate simulations where multiple parameters were used to determine the probability of range expansion. [a]AIC values are those of the Ordinary Least Squares regressions using re-scaled data to allow comparison with the AIC values from the Spatial Autoregressive models.

The ability of single predictor models to explain the global scale patterns remained limited, however, and it was only after incorporating interactions between parameters that the explanatory power increased substantially (Figure 3.3f; Table 3.1). According to both the OLS and UL regressions, the best model includes a combination of

temperature and precipitation and was able to explain almost 60% of the observed global scale variation (UL r^2=0.25) (Table 3.1). These key biological conclusions remained unaltered when accounting for spatial autocorrelation in model residuals (Table 3.1) and when using the alternative shape index (Appendix 2 Table S1).

3.4.4 Biogeographic realms

While the predictive power of the single variable models was limited at a global scale, analyses within biogeographic realms generally showed a marked increase in explanatory power (Table 3.2). For example, temperature explained 84% (UL r^2=0.35) of the spatial variation in range shape in the Neotropics compared to 23% at a global scale. This was accompanied by differences in the relative importance of environmental variables across biogeographic realms (Figure 3.4a; Table 3.2). For instance, while temperature was of primary importance in the Nearctic, precipitation and NPP were more important in the Afrotropics and Australia (Figure 3.4a; Table 3.2). The overall explanatory power of multivariate models also differed between realms, being highest in the Neotropics (r^2 = 0.89) and lowest in the Palearctic (r^2 = 0.02) (Table 3.2). The explanatory power of the within-realm models varied when using Maurer's Shape Index, but the biological conclusions remained qualitatively unchanged (Appendix 2 Table S2).

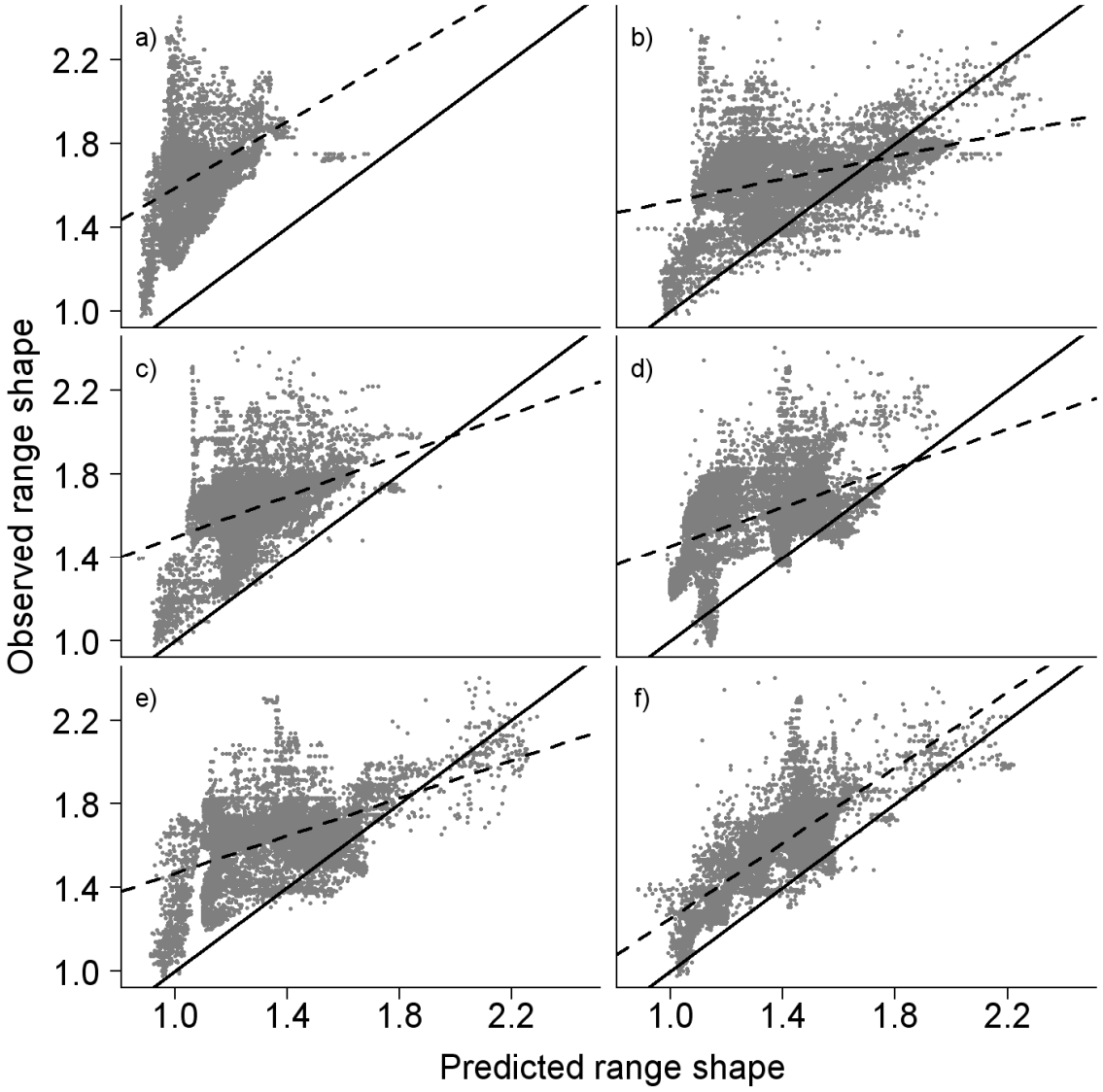


Figure 3.3. Observed against predicted spatial patterns in range shape measured using the Range Linearity Index (following log_e transformation). High values indicate linear species' distributions and low values more circular ranges. Cell values for the simulated data represent the average across 100 simulations. The dashed line is the fitted line from the Ordinary Least Squares regression. The black line is a slope of unity passing through the origin. Shown are the results for; (a) Null model, (b) Net Primary Productivity, (c) precipitation, (d) temperature, (e) elevation and (f) precipitation * temperature.

3.4.5 Range size quartiles

Finally, I tested whether the environmental drivers of range shape differed between rare and widespread species (Table 3.3). For species with smaller ranges (1st and 2nd quartile) elevation and precipitation were the strongest determinants of range shape, with NPP and temperature explaining relatively less of the variation (Figure 3.4b; Table 3.3). For widespread species (3rd and 4th quartile) the relative importance of NPP and temperature increased (Figure 3.4b; Table 3.3). The effect of incorporating the interaction between temperature and precipitation on the explanatory power of the simulations differed substantially according to range size (Table 3.3). For the first three range size quartiles, its effects were minimal, while for the largest quartile, the model explained three times as much variation as the best single predictor (Figure 3.4b; Table 3.3). Although the explanatory power of the models for each range size quartile varied when using Maurer's Shape Index, the biological conclusions again remained qualitatively unchanged (Appendix 2 Table S3).

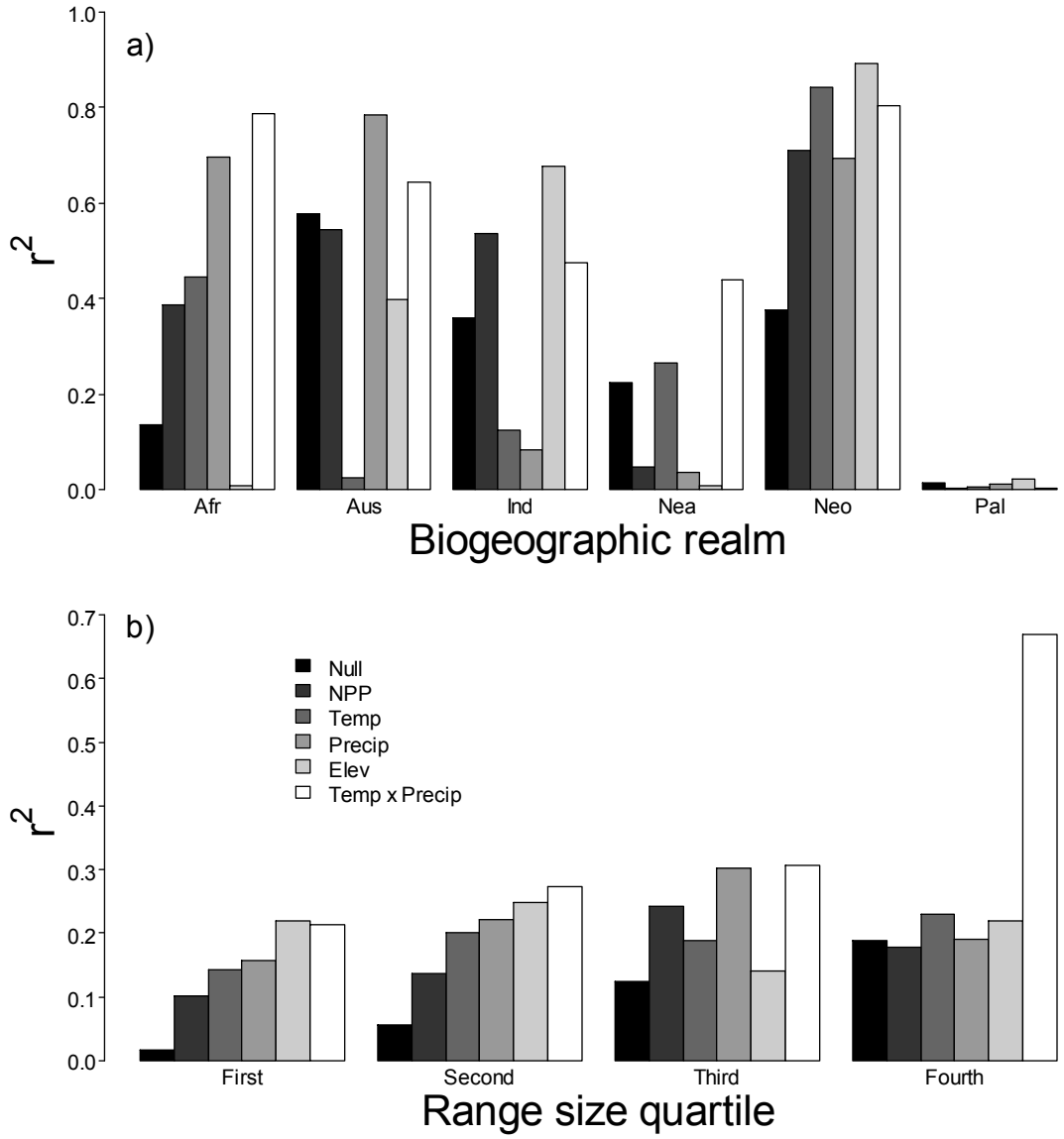


Figure 3.4. Explanatory power of models across realms and across range size quartiles. The height of the column shows the r^2 value from the Ordinary Least Squares regressions of observed against predicted spatial patterns in range shape, for each (a) biogeographic realm (excluding Antarctica and Oceania); Afrotropics (Afr), Australasia (Aus), Indomalaysia (Ind), Nearctic (Nea), Neotropics (Neo) and Palearctic (Pal), and (b) range size quartile (see Table 3.2 and Table 3.3 for actual r^2 values). Abbreviations of predictor variables are as follows: Net Primary Productivity (NPP), Precipitation (Precip), Temperature (Temp) and Elevation (Elev).

Predictor	Afrotropics				Australasia				Indomalaysia				Nearctic				Neotropics				Palearctic			
	Int	Slope	r^2	$r^{2\ b}$	Int	Slope	r^2	$r^{2\ b}$	Int	Slope	r^2	$r^{2\ b}$	Int	Slope	r^2	$r^{2\ b}$	Int [a]	Slope	r^2	$r^{2\ b}$	Int	Slope	r^2	$r^{2\ b}$
Null	0.18	1.51	0.13	0.00	-4.51	6.33	0.58	0.11	1.30	0.29	0.36	0.00	0.41	1.09	0.22	0.02	-0.01	1.47	0.38	0.09	1.49	0.18	0.01	0.00
NPP	1.12	0.33	0.39	0.15	0.49	0.68	0.54	0.40	1.09	0.32	0.54	0.15	2.05	-0.33	0.05	0.01	0.51	0.72	0.71	0.55	1.62	0.05	0.00	0.00
Precipitation	0.80	0.62	0.69	0.07	0.00	1.19	0.78	0.37	1.38	0.16	0.08	0.01	1.10	0.44	0.03	0.00	-0.47	1.54	0.69	0.38	1.54	0.12	0.01	0.00
Temperature	0.70	0.85	0.44	0.01	2.69	-1.22	0.02	0.01	1.00	0.38	0.12	0.09	-0.69	1.60	0.27	0.12	0.17	1.12	0.84	0.35	1.79	-0.08	0.01	0.00
Elevation	1.84	-0.14	0.01	0.00	-2.02	3.31	0.40	0.11	0.68	0.61	0.68	0.19	1.47	0.11	0.01	0.00	0.48	0.77	0.89	0.61	1.88	-0.15	0.02	0.00
TemperatureX Precipitation	0.72	0.68	0.79	0.08	-0.53	1.67	0.64	0.29	0.68	0.61	0.48	0.14	-0.16	1.29	0.44	0.14	0.29	0.93	0.80	0.53	1.84	-0.11	0.00	0.00

Table 3.2. Model results for each biogeographic realm from the non-spatial Ordinary Least squares and Unity Line regressions (excluding Oceania and Antarctica). Simulations were run on the global domain with species free to expand into adjacent realms if they were connected by land cells. The cells belonging to each realm were then analysed separately. Int = Intercept. r^{2} is from the OLS regression while $r^{2\ b}$ is from the unity line regression. Median values of range shape within each cell were log_e transformed prior to analysis.

Predictor	All species				First Quartile				Second Quartile				Third Quartile				Fourth Quartile			
	Int	Slope	r^2	$r^{2\,b}$	Int	Slope	r^2	$r^{2\,b}$	Int	Slope	r^2	$r^{2\,b}$	Int	Slope	r^2	$r^{2\,b}$	Int	Slope	r^2	$r^{2\,b}$
Null	0.79	0.80	0.16	0.01	0.94	0.38	0.02	0.01	0.98	0.46	0.06	0.03	0.80	0.70	0.12	0.04	0.66	0.94	0.19	0.02
NPP	1.25	0.27	0.13	0.03	0.10	0.55	0.10	0.10	0.14	0.59	0.14	0.12	0.24	0.56	0.24	0.17	0.18	0.32	0.18	0.05
Precipitation	1.01	0.49	0.15	0.03	0.29	0.86	0.16	0.14	0.35	0.89	0.22	0.17	0.14	1.12	0.30	0.17	0.96	0.53	0.19	0.04
Temperature	0.99	0.47	0.23	0.07	0.36	0.81	0.14	0.13	0.31	0.94	0.20	0.15	0.46	0.87	0.19	0.11	1.03	0.43	0.23	0.07
Elevation	1.02	0.45	0.25	0.07	0.48	0.66	0.22	0.21	0.52	0.73	0.25	0.22	0.93	0.48	0.14	0.09	1.00	0.47	0.22	0.06
TemperatureX Precipitation	0.35	0.90	0.59	0.25	0.34	0.79	0.21	0.20	0.24	0.94	0.27	0.23	0.32	0.93	0.31	0.21	0.32	0.92	0.67	0.30

Table 3.3. Model results for each range size quartile from the non-spatial Ordinary Least squares and Unity Line regressions. Int = Intercept. r^2 is from the OLS regression while $r^{2\,b}$ is from the unity line regression. Median values of range shape within each cell were log_e transformed prior to analysis.

3.5 Discussion

Here I show that the shapes of avian ranges exhibit striking patterns of geographical variation and that these patterns can be well predicted by relatively simple models of range expansion limited by a few key climatic variables. In addition, more detailed analyses identified strong differences between regions and between rare and widespread species with respect to the factors constraining range expansion. The results also showed that random models of range growth, while still giving rise to geographical variation in range shape, were unable to account for these patterns. These biological conclusions were robust irrespective of the method used to quantify variation in range shape.

The finding that much of the spatial variation in geographic shape can be predicted using climate-driven models of range expansion provides global confirmation for the many studies on avian range limits at smaller taxonomic and geographic scales (Gaston 2003; McInnes et al. 2009; Root 1988a; Root 1988b). Niche modelling studies have also found a strong association between bird species' ranges and environmental gradients but have been criticised for failing to model the mechanisms underpinning this relationship (Guisan & Zimmermann 2000). Indeed, it has even been argued that such associations could arise solely as an artefact of the similar spatial structures present in the data (Bahn & McGill 2007; Beale et al. 2008). Using an alternative more mechanistic approach I show that the strong signal of the environment in shaping species' ranges cannot arise by chance. Recent claims that species' distributions are uncoupled from

climate (e.g. Beale et al. 2008) therefore do not appear to be a general feature of avian ranges.

The individualistic nature of species' niches may be expected to lead to little generality in the causes of range limits across large taxonomic groups (Colwell & Lees 2000; Lyons & Willig 1997; Ricklefs 2008). Furthermore, a strong role for biotic interactions in limiting distributions (MacArthur 1972) is generally expected to weaken the match between the geographic range and the broad scale environment (Huntley et al. 2004). It was beyond the scope of this study to try and tease apart the relative role of the direct effects of climate on range limits as opposed to those mediated through biotic interactions. However, the predictability I find in the configuration of species' ranges at continental scales suggests that the high dimensionality in the proximate causes of range limits can be collapsed along a small number of spatially independent climatic axes. Brown et al (1996) reached a similar conclusion regarding the spatial distribution of abundance within species' ranges. These findings may explain why the fit of niche modelling studies appears to be independent of trophic level (Huntley et al. 2004) and supports the use of ensemble approaches to the study of species richness gradients and the impacts of environmental change (Gotelli et al. 2009).

Grinnell (1914; 1917) proposed a hierarchical arrangement in the importance of the environmental factors governing species' distributions, starting with temperature, followed by humidity and finally features of the local habitat, such as food supply. At a global scale across all birds, the findings of this study are broadly consistent with this simple hierarchy, with temperature, precipitation and, NPP controlling range shape in

descending order of importance. Elevation, a surrogate for fine scale environmental gradients, had a similar explanatory power to temperature. The results show that elevation gradients are stronger predictors of range shape in the tropical mountain ranges of the Andes and Himalayas, supporting the idea that changes in elevation represent stronger barriers to dispersal in the tropics (Janzen 1967). The explanatory power of the single predictor models was low at a global level because different environmental factors were responsible for constraining distributions in different biographic realms. For instance, moisture related variables were of greater importance in tropical and southern hemisphere realms where temperature (at least in the lowlands) is less likely to be limiting, with the reverse true at northern high latitudes (Terborgh 1973). Restricting the analyses to individual realms therefore resulted in substantial increases in the explanatory power of the models.

The variation between geographic realms in the drivers of geographic range shape closely mirrored the latitudinal (Hawkins et al. 2003) and inter-realm heterogeneity in the correlates of species richness (Davies et al. 2007). Differences in the dominant factors structuring species' distributions across range size quartiles are also broadly consistent with the findings from studies on species richness (Jetz & Rahbek 2002; Rahbek et al. 2007). For instance, temperature was the principal predictor of range shape only for widespread species, with precipitation and in particular elevation more closely associated with range restricted taxa. A correspondence between the factors driving richness and range shape is not a necessity. Species could show strong turnover across climatic gradients but exhibit no trend in richness, while patterns in richness could arise from processes unrelated to those structuring geographic ranges (Currie et al. 2004). The

results suggest a strong coupling between the determinants of range shape and richness, supporting the idea that limits to range expansion underlies large scale richness gradients (Currie et al. 2004).

Geometric constraints on the location of geographic ranges arising from continental edges have been put forward as an explanation for large scale gradients in species diversity (Colwell & Lees 2000; Jetz & Rahbek 2001). This hypothesis has proven controversial, however, and analysis of the predicted patterns of species richness has failed to resolve the debate (Storch et al. 2006). Here I show that although continental boundaries do have a discernable effect in shaping geographic ranges, their independent role is small compared to that of environmental gradients (Grinnell 1914).

The results show that, at a broad spatial scale, simple climatic models are better at predicting range shape patterns for widespread than endemic species. Studies on species richness have similarly found only a weak association with climatic drivers and hotspots of endemic taxa (Jetz & Rahbek 2002; Rahbek et al. 2007). The results suggest that issues of scale may be partially responsible (Hawkins & Diniz-Filho 2006). For instance, the extreme linearity of the ranges in the Andes arising from the steep climatic gradients were under predicted by the simulations (Graves 1988). In other cases, habitat affinities more loosely connected to the climate appear to be responsible. For instance, 15% of the non-aquatic birds within the Amazon basin are linearly distributed along the seasonally flooded habitats along the Amazon River (Remsen & Parker 1983) and were not predicted by the models based on the regional climate. Incorporating such additional

variables, and at finer spatial resolutions, would be expected to improve the explanatory power of the models.

The simulations were based on a simple model of range expansion (Jetz & Rahbek 2001; Rahbek et al. 2007; Storch et al. 2006), yet geographic ranges are known to be dynamic through time (Dynesius & Jansson 2000). Departures from the spreading dye model may explain why the simulations had lower explanatory power in northern high latitude realms where recent fluctuations in species' ranges have been particularly dramatic (Dynesius & Jansson 2000). Across the environmental models, the linearity of species' ranges was under-predicted; most simulated values fall above the line of unity. In addition to the issues of scale discussed above, I suspect that this may be caused because local extinction was excluded from the models. When ranges are simulated purely by a process of accretion, then even unfavourable cells have a good chance of being colonised if they are adjacent to cells that were occupied early in the simulation. This results in ranges bleeding across environmental gradients. As a result, I expect that allowing occupied cells to go extinct with a probability determined by environmental suitability, would improve the match between the observed and simulated patterns.

How sensitive are these conclusions to the choice of index used to measure range shape? Most of the results were qualitatively unaltered by measuring ranges using either the Range Linearity or Maurer's Shape Index. However, the relative explanatory power of the environmental and stochastic models did, in some cases, differ depending on the index used. The most notable difference was that for the global models, Maurer's Index improved the fit of the null and temperature based models while the fit for the other

variables was diminished. These differences arise because the environmental gradients, and thus the resulting ranges, differ in their spatial complexity and the two shapes indices differ in their ability to account for this. For simple shapes both indices give similar values, but when species have contorted and irregular distributions, Maurer's Index substantially underestimates range elongation compared to the Range Linearity Index. As a result, when range expansion occurs at random or along latitudinal temperature bands, the explanatory power of Maurers' Index is inflated, whereas the importance of environmental gradients that do not produce such simple range shapes (e.g., precipitation) are underestimated. Sandel (2009) recently compared the predictions of a model of random range growth to observed patterns of range shape in the New World, measuring range shape using simple latitudinal and longitudinal extents. The study found a much higher explanatory power for the null model than that found here. The results of this study suggest that using indices of range shape that are insensitive to the complexities of geographic distributions are likely to overestimate the role of stochastic processes in limiting range expansion and lead to biases in the relative explanatory power of deterministic models.

3.6 Conclusion

In conclusion, I show that there is striking geographical variation in the shape of bird species' ranges and that these patterns provide an opportunity to test the environmental factors, and the role of stochastic processes, in structuring geographic ranges. The results of this study extend our understanding of the factors limiting species' ranges by placing the many previous more taxonomically and spatially restricted studies on range limits in a

global context. By providing a more mechanistic test of the environmental determinants of range limits the results give reason for cautious optimism in attempts to predict broad scale patterns in the future distribution of biodiversity.

Chapter 4

Speciation, extinction, and the illusion of range size trajectories in reconstructed phylogenies

4.1 Abstract

A number of studies have attempted to infer the evolutionary dynamics of geographic ranges using range sizes and ages of extant species estimated from reconstructed phylogenies. However, the relationship between range size and evolutionary age is also likely to be influenced by past speciation and extinction events and ignoring these processes may therefore lead to biased inferences regarding the evolutionary dynamics of geographic ranges. Here I use simulations and estimates of the geographic range sizes and ages of ca 1300 species of mammals and birds to test whether there is any evidence for systematic range evolution in these groups. In almost half of all bird and mammal clades (genera and orders) examined, range size was dependent on evolutionary age, either increasing or decreasing. Such patterns are often interpreted as evidence for systematic changes in range sizes through time. However, the simulations showed that these patterns are expected even when ranges fluctuate randomly in size due to the effects of speciation and extinction. If extinction rates are higher for species with small geographic ranges this leads to a positive relationship between range size and

evolutionary age. Speciation can lead to positive, negative or flat relationships between range size and age depending on the asymmetry of range division and the affect of range size on the chances of speciation. Furthermore, the proportion of observed clades exhibiting range size-age correlations did not differ from that expected under these null models. These results show that the relationship between evolutionary age and range size in reconstructed phylogenies provides a misleading picture of the mode of geographic range evolution. Range evolution in birds and mammals appears to be consistent with a model in which range sizes have fluctuated randomly through time.

4.2 Introduction

It is well established that species' geographic ranges are dynamic through time (Davis & Shaw 2001; Dynesius & Jansson 2000; Lessa et al. 2003). What is less clear is whether these dynamics follow any systematic trajectories or whether changes in range size are largely unpredictable. That geographic ranges may exhibit systematic trends over the course of a species life time has been proposed a number of times. In perhaps the earliest model, Willis (1922) argued that in tropical plants, with very limited dispersal, range size should gradually expand through time as new areas are colonised. Such slow incremental expansion is now often regarded as being an unlikely scenario, given the rapid spread of species introduced to new regions observed over recent decades (e.g. Grosholz 1996). Following an initial phase of expansion, other models predict that ranges remain at a stable size for long periods of time reflecting the extent of the habitats or region within which a species occurs (Jablonski 1987). Alternatively species may embark on a gradual

phase of contraction towards extinction, a model termed the "taxon cycle" (Ricklefs & Cox 1972; Wilson 1961). It has been argued that the decline phase of the taxon cycle may be driven by asymmetric competition between species arising from the co-evolutionary dynamics between hosts and their parasites (Ricklefs 2010; Ricklefs & Bermingham 1999; Ricklefs & Cox 1972). Such declines have also been explained in terms of the greater number of negative biotic interactions reducing the fitness of species with large ranges (Liow & Stenseth 2007).

Another possibility, often regarded as the null model, is that changes in geographic range size occur at random through time (Gaston 1998). Hubbell's (2001) neutral theory predicts that species' abundances, and thus geographic ranges, drift randomly in size due to the stochastic dispersal and death of individuals. However, a pattern of random range evolution does not require the assumptions of neutrality or an absence of the ecological and historical factors known to limit species' distributions (Grinnell 1914; Kellermann et al. 2009; Price & Kirkpatrick 2009; Root 1988b) (Chapter 3). Random changes in range size could arise if these ecological and historical factors vary stochastically and independently through time (Raup et al. 1973). For instance, fluctuations in range size over evolutionary time could be driven by the removal or appearance of geological barriers (Weir et al. 2009), the extinction or invasion of an enemy (Channell & Lomolino 2000), rare long distance dispersal events (Carlquist 1981) or the appearance of new mutations conferring resistance to pathogens (Ricklefs 2010) or greater climatic tolerance (Wiens & Donoghue 2004).

Evidence in support of different models of range evolution is most readily obtained from taxa with good fossil records where the range size of individual lineages

can be traced through time (Foote et al. 2008; Foote et al. 2007; Jablonski 1987; Jablonski et al. 2006; Liow et al. 2010; Liow & Stenseth 2007). However, where the fossil record is missing, insights into past range dynamics may still be possible using the ranges of extant species represented in reconstructed phylogenies (Ree et al. 2005; Ree & Smith 2008). One common approach is to estimate the ages of species from the phylogeny as the time since divergence from the closest extant relative. If geographic ranges exhibit predictable trajectories through time then the range size of species of different ages should vary in a way that reflects these temporal changes (Jones et al. 2005; Paul et al. 2009; Webb & Gaston 2000; Webb et al. 2001; Willis 1922). Using this approach, Ricklefs and Bermingham (1999; 2002) found that within the Lesser Antilles, young species of bird were widespread while old species were restricted to single islands. This pattern was interpreted as supporting the taxon cycle model (Wilson 1961). Webb and Gaston (2000), using a selection of bird genera, found a variety of patterns between range size and evolutionary age, including positive and humped relationships implying either a gradual increase in range size with evolutionary age or a rapid increase followed by a gradual decline. Jones et al (2005) showed that range size and evolutionary age were negatively correlated amongst primates and carnivores, also taking this as evidence for a model of rapid expansion and protracted contraction. Finally, Paul et al (2009) identified a positive relationship between range extent and the ages of species in a genus of Amazonian plants, interpreting this as evidence of Willis' (1922) model of gradual range expansion.

While the particular model of range evolution supported by these studies varies, in each case the authors reject random evolution of ranges as an explanation for observed

age versus range correlations (Jones et al. 2005; Webb & Gaston 2000; Webb et al. 2001). This is based on the rejection of the standard statistical null model that range size is independent of evolutionary age (Webb & Gaston 2000). However, this relationship is also likely to depend on the effects of speciation and extinction (Weir & Schluter 2007). For instance, if small geographic range size is associated with a higher probability of extinction (Foote et al. 2008; Jablonski 1995; Jablonski & Hunt 2006), then this could give rise to a positive relationship between range size and evolutionary age. Equally, if large geographic range size promotes speciation (Brown 1957; Gavrilets et al. 2000; Jablonski & Roy 2003; Rosenzweig 1975; Rosenzweig 1978), then the ages of species may decline with range size. As a result, under a biologically realistic null model of random range evolution, range size and evolutionary age need not be independent. Ignoring the role of speciation and extinction may therefore lead to spurious conclusions regarding the evolution of species' ranges within lineages.

Here I test whether there is any evidence from reconstructed phylogenies for systematic changes in range size through time. I use estimates of species ages and range sizes from extant mammals and birds and compare these observed patterns to those arising from simulations in which range sizes evolve randomly through time. Within these simulations I investigate the effects of variation in the rate of range size evolution, extinction and the geographic mode and rate of speciation on the expected patterns. I show that a significant relationship between range size and evolutionary age is present in almost half the clades of birds and mammals examined. However, the confounding effects of speciation and extinction mean that this cannot be reliably interpreted as evidence for systematic changes in range size through time. Instead the patterns in birds

and mammals appear to be consistent with range sizes having evolved randomly through time.

4.3 Methods

4.3.1 Observed data

I investigated the relationship between range size and evolutionary age in mammals and birds because these groups have featured prominently in studies attempting to infer patterns of range evolution from extant phylogenies (Jones et al. 2005; Webb & Gaston 2000). In addition, as compared with other taxa, there is abundant information on their geographic distributions (Orme et al. 2006; Schipper et al. 2008) and phylogenetic relationships (Bininda-Emonds et al. 2007; Phillimore & Price 2008). I selected genera for which mitochondrial protein coding genes had been sequenced for more than 80% of species. Sequences were downloaded from GenBank using GENEIOUS (Drummond et al. 2006) and aligned by eye in MEGA v4 (Kumar et al. 2004). Trees were constructed according to a relaxed clock Bayesian method in BEAST v1.5.4 (Drummond & Rambaut 2007). The high level of taxon sampling was necessary to reduce the overestimation of species ages resulting from missing species. The selection of bird clades is largely based on the genus level phylogenies in Phillimore and Price (2008) (see Chapter 2), but where possible I included more genes, and sequences for missing species according to Sibley and Monroe (1990). If an initial search suggested sufficient sequence data was available, I also expanded the sampling to construct family level trees. This allowed me to include

species poor clades that may exhibit unusual dynamics but are usually excluded from studies focusing solely on more diverse groups (Ricklefs 2005).

In BEAST, I used a Yule prior on branching times and an HKY model of substitution with 4 gamma categories and separate rates for codon positions 1+2 versus 3. Rate variation amongst branches was assumed to be uncorrelated and drawn from a log-normal distribution. Rates of molecular evolution are known to vary substantially amongst mammalian lineages (Weir & Schluter 2007; Welch et al. 2008) and so for each clade, trees were dated using fossil calibrations obtained from the literature. For birds I assumed a molecular clock of 1% per lineage per million years, as fossil calibration points are rare and this rate is thought to hold across most avian clades (Weir & Schluter 2008). On all calibrations I used a lognormal prior with a mean and standard deviation of 1 and with the minimum age set to that used in the original study; usually corresponding to the first appearance of a group (Ho & Phillips 2009).

I performed two runs of 5-10 million generations depending on the time required for convergence as assessed in Tracer v1.4 (Rambaut & Drummond 2007). The first 10% of the generations were discarded as burn-in and then, depending on the length of the model run, sampled every 4000-8000 generations to produce a posterior distribution of 1125 trees. The trees were combined from the separate runs and summarised as the maximum clade credibility tree. From these trees I estimated the absolute ages of species (my) as the tip length corresponding to each extant species. For the family level trees I excluded any species belonging to; (i) genera less than 80% complete, (ii) complete genera that were polyphyletic with genera <80% complete and (iii) monotypic genera if <80% of the other genera in the clade had been sequenced.

In total I obtained estimates of species' range sizes and ages for 1271 species, representing 212 genera and 17 orders. Range sizes (km^2) for the species were taken from Orme et al. (2006) and Schipper et al. (2008). Previous studies have investigated the relationship between range size and evolutionary age either within genera (Webb & Gaston 2000) or entire orders (Jones et al. 2005). It is unclear what, if any, is the most appropriate taxonomic level to test for patterns in range size evolution. Small taxa may have weak power and exhibit greater stochasticity while larger taxa may include heterogeneous patterns of range size dynamics. As a result, here I examined the relationship between range size and evolutionary age across both genera and orders – in most cases, families are only represented by a single genus and so this taxonomic level is not informative. Genera were defined according to standard avian and mammalian taxonomies (Sibley & Monroe 1990; Wilson & Reeder 2005) except where the phylogenetic hypothesis disagreed with taxonomy. I then used the phylogenies to assign the species to a particular genus. Only genera with more than 5 species were included in the generic level analysis, while all species were included in the order level analysis.

4.3.2 Range size simulations

Range evolution (σ^2) and extinction: I simulated phylogenies in which range sizes evolve in discrete time according to a random walk, and where each simulation lasts for 200 time units (t). At t = 0, a range size was drawn at random from the observed range size of birds and mammals (median = 1.2×10^6 km^2). At each time step, a random normal deviate was then added to the current species' range size (mean (μ)= 0, variance (σ^2) = 1

x 10^4, 1 x 10^6, 1 x 10^8, 1 x 10^{10}, 2.25 x 10^{10}, 4 x 10^{10}). These values were chosen to model cases of both stasis in range size (σ^2= 1 x 10^4), and rapid range size fluctuations (σ^2= 4 x 10^{10}). Under the most rapid fluctuations, a species with a range size equivalent to the average observed across birds and mammals would increase or decrease in range size by on average 11% each time step. The stochastic fluctuations in range size may result in the area of the species' range declining to zero, whereupon it becomes extinct and is removed from the simulation. I note here, that this model assumes that the absolute loss or gain of area is independent of range size. A model in which fluctuations in range size occur as a proportion of range size could have been used, but this would have required setting an arbitrary range size threshold below which species are deemed to have become extinct. In addition, I do not expect that this alternative model would qualitatively alter the main findings of the simulations. For instance, range size would remain negatively correlated with extinction probability (see below) albeit with a shallower slope.

Speciation (λ): At each time step of the simulation, a species could undergo speciation with a probability (λ) that was either dependent or independent of range size. In the absence of information on the exact form of the relationship between range size (e.g., see Chapter 2) and speciation probability I assumed that λ was a positive linear function of range size (Rosenzweig 1978) with an intercept of zero and a slope calculated to give a maximum speciation probability of 1.0 at ranges equal to or greater than the maximum observed range size of mammals and birds (6.2 x 10^7 km^2). I also investigated the effects of assuming smaller values of maximum λ (Max λ = 0.5 and 0.2 per lineage/time unit). Most species in fact had much lower chances of speciating than these maximum values

would suggest because of the right skewed distribution of range sizes. Because most species have small geographic ranges this simple linear model is expected to produce similar results to more complicated scenarios in which λ peaks at intermediate range sizes, as may arise under certain probabilistic models of geographic isolation (Chapter 2; Rosenzweig 1978).

I also investigated scenarios in which λ was independent of range size, exploring values of λ = 0.014, 0.02 and 0.03. These values were chosen to bound the median probability of speciation expected in the range size dependent speciation model assuming that ranges sizes in these simulations were equivalent to those observed for mammals and birds. I did not explore the possibility that λ declines with range size because this is generally only expected if factors correlated with range size inhibit speciation, rather than the effects of range size *per se* (Gavrilets et al. 2000; Jablonski & Roy 2003). Nevertheless I expect that a negative relationship between range size and λ would lead to qualitatively similar results to those arising in the range size independent speciation model (see 4.5 Discussion).

Range division (β): At each speciation event the parental range size (A_p) was divided amongst the two daughter species (Anderson & Evensen 1978; Waldron 2007). I investigated models of varying asymmetry in range division by randomly selecting one daughter and drawing its range size (A_{d1}), as a proportion of A_p, from a beta distribution (α=1, β = 1, 5 and 10). The range size of the other daughter (A_{d2}) was then assigned as $A_{d2} = 1 - A_{d1}$. To obtain the absolute range sizes of the daughters, A_{d1} and A_{d2} were then multiplied by A_p. When $\beta = 1$, this is a uniform distribution, equivalent to that arising

under a broken stick model (Barraclough & Vogler 2000; Waldron 2007). With higher values of β the range sizes of the sisters become more asymmetric. When β=10, on average one daughter species will inherit a range size 7% of the parental range while the other retains 93% of the parental range. This highly asymmetric range division can be regarded as approximating a peripatric model of speciation, in which a small peripheral isolate is formed from the dispersal of a few individuals beyond the parent range (Chapter 2; Mayr 1963). These models of range splitting were chosen to encompass a wide variety of possible range inheritance scenarios rather than assuming a particular model of range division (Waldron 2007).

Parameter	Starting values
Maximum speciation probability (Max λ)	1, 0.5, 0.2, 0.03, 0.02, 0.014
Dependence of speciation probability (λ) on range size (rsλ)	0, +
Range split asymmetry (β)	1, 5 ,10
Rate of range evolution (σ2)	$1x10^{4}$, $1x10^{6}$, $1x10^{8}$, $1x10^{10}$, $2.25x10^{10}$, $4x10^{10}$

Table 4.1 Parameters used in the simulations

Extracting the simulated data: At the end of each simulation run (t = 200) I recorded the size of the geographic ranges of the extant species and calculated their ages from their phylogenetic relationships. For each combination of parameter values I performed 5000 simulations, contingent on the survival to the end of the simulation. For these successful simulations I also recorded the range sizes and ages of species extant at t = 50 and t =

100, in order to investigate the effects of simulation length on the expected patterns. The different combinations of parameter values explored in the simulations are given in Table 4.1.

4.3.3 Analysis

For both the observed and simulated clades, I fitted linear and polynomial ordinary least squares regressions of evolutionary age against range size. Both variables were log-transformed to improve normality in the residuals. Under this framework there are seven possible statistical models describing the relationship between evolutionary age and range size. The parameters and shapes of these Range Evolution Models (REM's) are given in Table 4.2. For each of the observed and simulated clades the best REM was selected as the model with the lowest AIC.

To explore the general relationship in the simulations between evolutionary age and range size under different parameter combinations, I calculated simple linear regressions across the pooled data from all 5000 replicates. In order to establish whether the frequencies of the 7 REM's observed across bird and mammal genera differed from the null expectation, I randomly drew 65 simulated clades and allocated these to REM categories based on AIC. I repeated this procedure 100 times in order to generate confidence intervals on the expected relative frequencies of the REM's.

REM	slope coefficient	polynomial slope coefficient	curve shape
1	0	Na	
2	+	Na	
3	-	Na	
4	+	+	
5	-	+	
6	+	-	
7	-	-	

Table 4.2 Range evolution models (REM's). Models were fitted using standard linear and polynomial regressions with the best model selected as the model with the lowest AIC.

4.4 Results

4.4.1 Observed data

Of the 65 genera of mammals and birds containing more than 5 species, in 28 of these the best range evolution model was one in which range size was dependent on evolutionary age (REM 2-7) (Figure 4.1a; Appendix 3 Table S1). For the remaining 37 clades the best model was one in which there was no association between the range sizes and ages of species (REM 1). Of the 17 orders, range size was dependent on evolutionary age in 9 of the clades (Figure 4.1b; Appendix 3 Table S1). In cases where range size was dependent on age, the most common relationship was a monotonic increase in range size with evolutionary age (REM 2) (Figure 4.1a, b; Appendix 3 Table S1).

At the genus level all range evolution models were selected at least once, while at the order level REM 3 (monotonic decline) was not selected at all (Figure 4.1a, b;

Appendix 3 Table S1). For instance, in Rodentia range size increased monotonically with evolutionary age (REM 2) (Figure 4.2a), while in Craciformes there was evidence for an initial increase followed by a gradual decline in range size with evolutionary age (REM 7) (Figure 4.2b; Appendix 3 Table S1). In Passeriformes, range size increased gradually with the ages of species, but there was also evidence for a levelling off or decline in range size amongst the oldest species (REM 6) (Figure 4.2c; Appendix 3 Table S1). In Primates, the best model supported an initial decrease and then increase in range size with evolutionary age (REM 5) (Figure 4.2d; Appendix 3 Table S1).

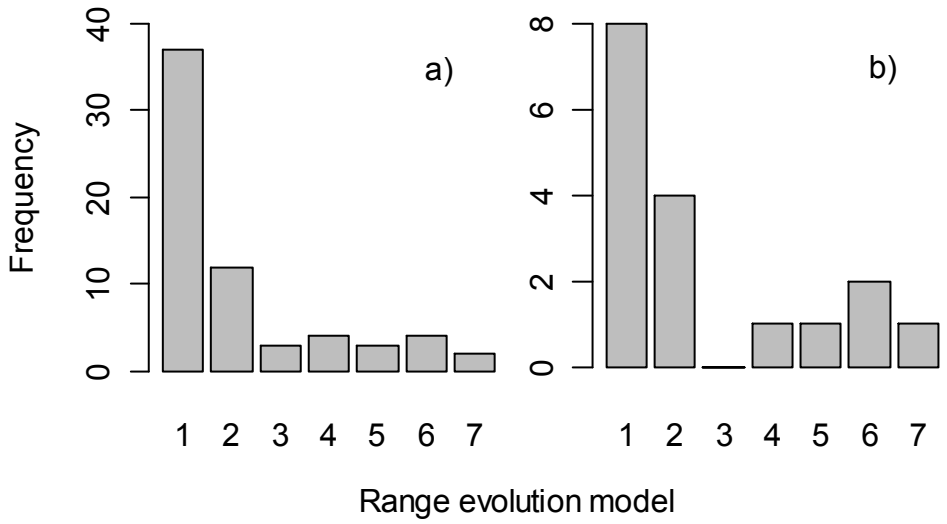


Figure 4.1 The frequency with which each range evolution model (REM) is selected as the best model in birds and mammals across a) 65 genera and b) 17 orders. REM models were fitted using standard linear and polynomial regressions with the best model selected as the model with the lowest AIC (see Table 4.2 for REM curve shapes).

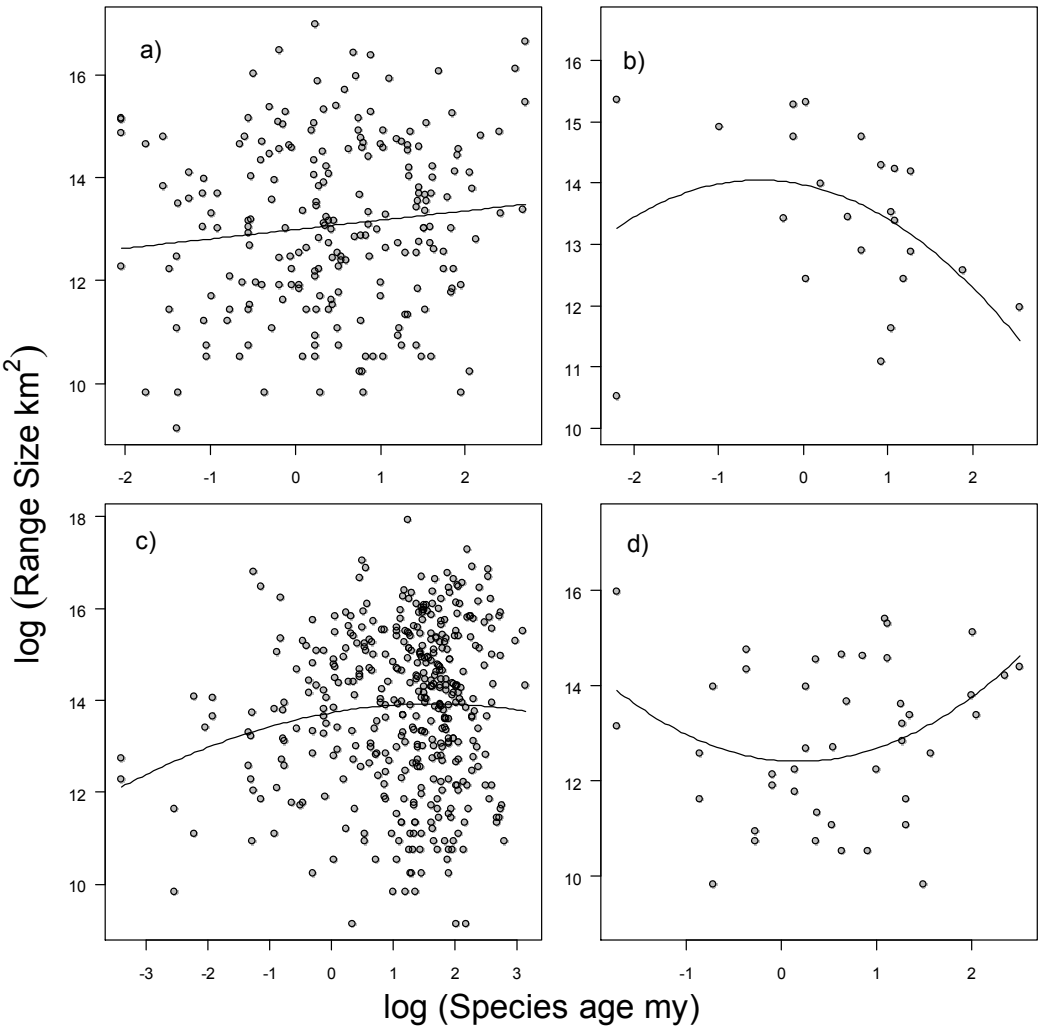


Figure 4.2. The relationship between evolutionary age and range size across four example avian and mammalian orders a) Rodentia, b) Craciformes, c) Passeriformes, d) Primates. The fitted curve corresponds to the range evolution model (REM) with the lowest AIC. Both species range sizes and ages were log-transformed.

4.4.2 Range size simulations - pooled results

Simulations showed that the relationship between evolutionary age and range size varied substantially depending on the initial starting parameters, and that these parameters often interacted in complex ways to alter the expected patterns. The maximum probability of speciation (Max λ) and the simulation length did not qualitatively alter the conclusions and so here I only present results using intermediate λ values and for the full simulation length.

The results from 4 pooled sets of simulations with different starting parameters are presented in Figure 4.3. While in some cases ranges sizes were independent of evolutionary age, in others the relationship between range size and evolutionary age was negative (Figure 4.3a) or positive (Figure 4.3b,d). This occurred despite the fact that ranges had no underlying tendency to either expand or contract in size through time. Varying σ^2 had a dramatic effect on the expected slope between evolutionary age and range size (Figure 4.4). While flat and negative slopes are possible under stable range sizes, increasing σ^2 leads to the slopes becoming increasingly positive (Figure 4.3b; Figure 4.4). This is because rapid range evolution results in species with small geographic ranges quickly drifting to extinction. So, while young species can have ranges of any size, species can only persist for long enough to become old by virtue of a large geographic range.

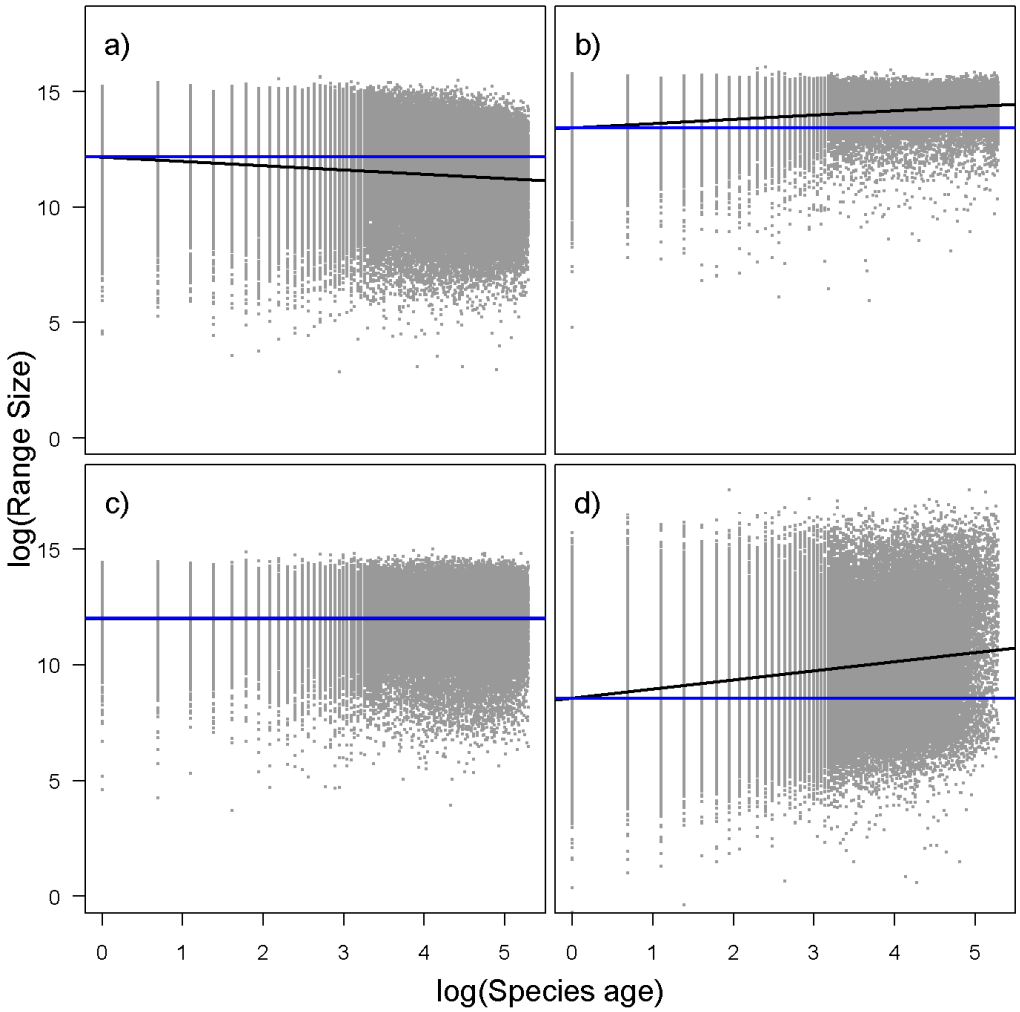


Figure 4.3 The relationship between evolutionary age and range size from four sets of 5000 simulation runs. Outputs differ according to the rate of range evolution (σ^2), range split asymmetry (β) and relationship between range size and speciation probability ($rs\lambda$) a) $\sigma^2 = 1x10^4$, $\beta = 10$, $rs\lambda = +$, b) $\sigma^2 = 2.25x10^{10}$, $\beta = 10$, $rs\lambda = +$, c) $\sigma^2 = 1x10^4$, $\beta = 1$, $rs\lambda = +$, d) $\sigma^2 = 1x10^4$, $\beta = 10$, $rs\lambda = 0$. The black line is from the OLS regression of log(Area km^2) on log(Age time units). To highlight the departure of these expected results from the standard statistical null model, the blue line has been drawn with the same intercept as the fitted curve but with a slope of zero.

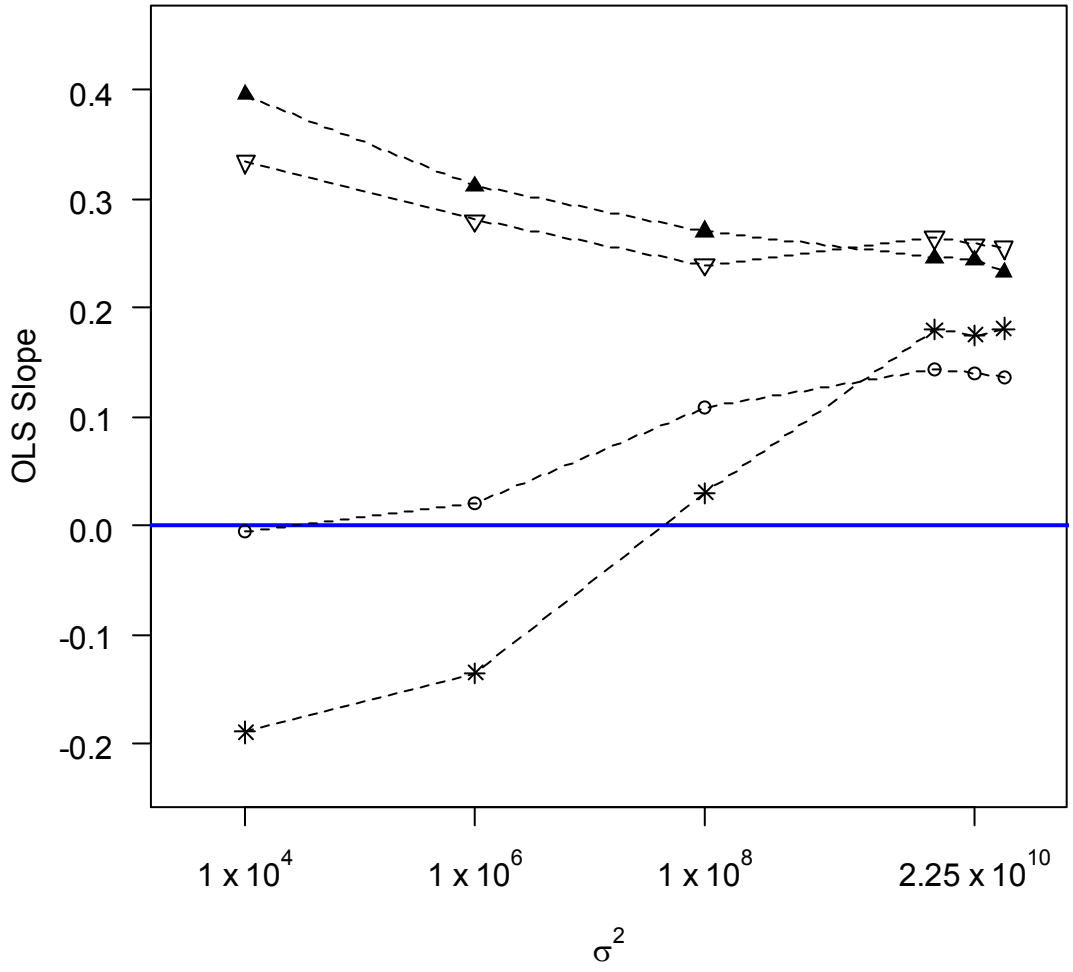


Figure 4.4 Variation in expected slope between evolutionary age and range size in response to variation in the rate of range evolution (σ^2) and speciation parameters. Each point shows the linear OLS slope fitted to the results from each pooled set of 5000 replicate simulations runs. The solid blue line indicates a slope of zero, where range size is independent of species age. Different symbols correspond to different speciation parameters; range split asymmetry (β) and dependence of speciation probability on range size (rsλ) * (β = 10, rsλ = +), ° (β = 1, rsλ = +),▽(β = 1, rsλ = 0), ▲ (β = 10, rsλ = 0). Note that σ^2 is plotted on a log-scale.

When σ^2 is small then the slope of the relationship between evolutionary age and range size becomes highly sensitive to both β and whether λ varies with range size. When range splitting is asymmetric (β=10), and λ increases with range size, then a negative relationship between evolutionary age and range size is expected (Figure 4.3a; Figure 4.4). This is because species with large geographic ranges have higher rates of speciation and will thus tend to occur on short terminal branches. Species with small geographic ranges can instead be either young or old. In contrast, if range inheritance is more symmetric (β=1), a flat relationship between range size and evolutionary age is expected (Figure 4.3c; Figure 4.4). This is because the equal splitting of the parental range amongst the two daughter species erodes the signal of the relationship between range size and λ (Chapter 2).

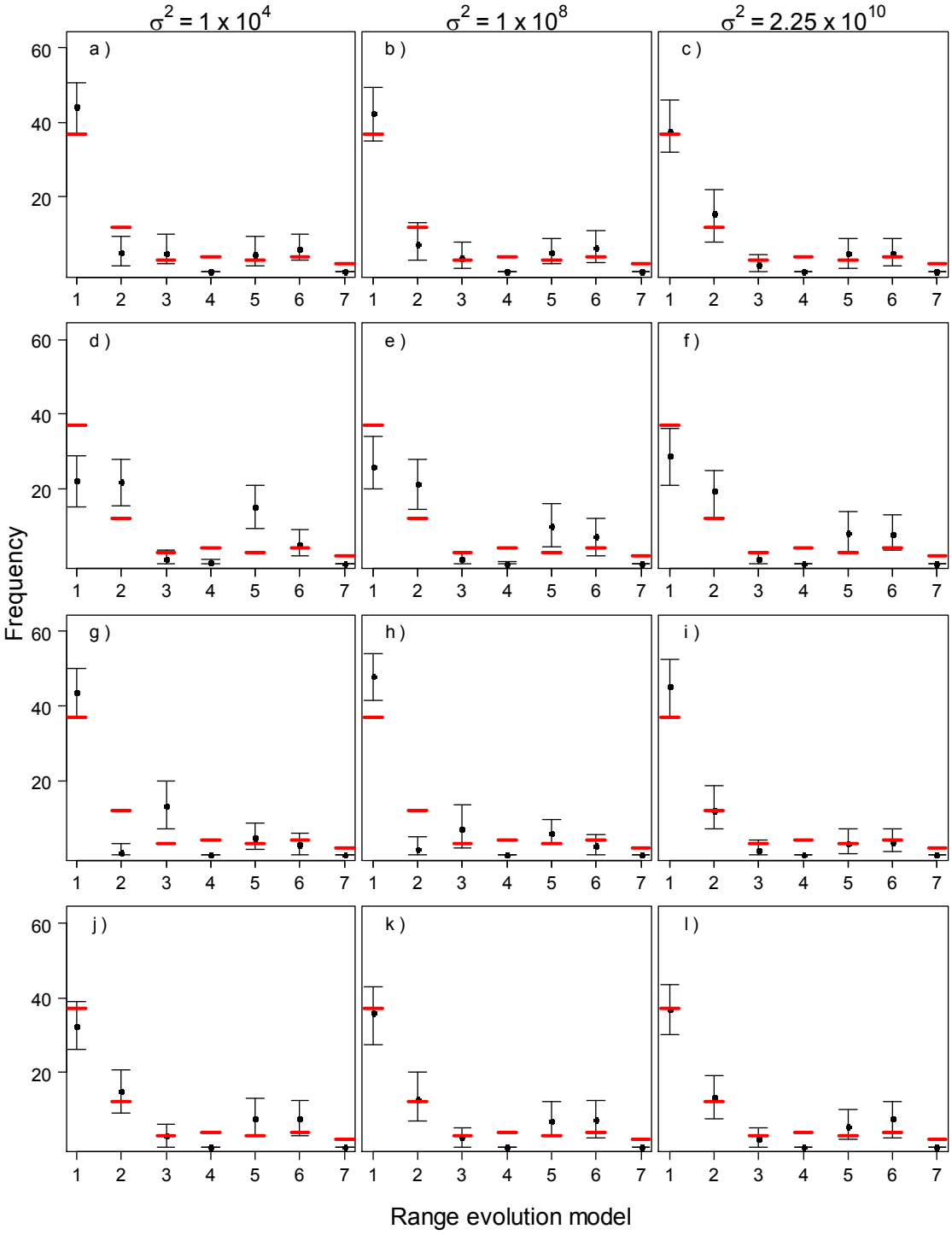
When $rs\lambda = 0$ then these patterns are altered. Under this scenario, the slope of the relationship between evolutionary age and range size is positive regardless of the value of σ^2 (Figure 4.3d; Figure 4.4). This is because young species are those which have recently arisen from a range splitting event and are therefore likely to have smaller ranges than older species which have not recently been split. In this scenario, higher values of σ^2 lead to flatter slopes between evolutionary age and range size by dampening this signal of speciation (Figure 4.4). Nevertheless the relationship between range size and evolutionary age remains positive (Figure 4.4).

4.4.3 Comparing the simulated and observed results

Similar effects of varying the initial parameter values are evident when the relationship between evolutionary age and range size is analysed for each replicate simulation run separately (Figure 4.5). For instance, holding other parameters constant but increasing σ^2, leads to a greater frequency of clades exhibiting a positive relationship between range size and evolutionary age (REM 2) (Figure 4.5 a-c). Holding σ^2 constant but increasing β, leads to a higher frequency of negative slopes between range size and evolutionary age (REM 3) (Figure 4.5 a,d). Perhaps the most important insight revealed by the individual clade analysis, however, is the variation in possible model outcomes within each region of parameter space (Figure 4.5). Although the pooled results showed that the expected relationship between range size and evolutionary age was often positive or negative (Figure 4.4), the most frequently selected model across simulations was in fact one in which there was no association between evolutionary age and range size (REM 1) (Figure 4.5). This highlights the important role of stochasticity and sample size in causing deviations from the expected relationship. Nevertheless in a large proportion of clades, range size did vary with the ages of species (Figure 4.5). In scenarios in which $rs\lambda=0$, over 60% of simulation runs showed a positive (REM 2) or peaked relationship between evolutionary age and range size (REM 5,6) (Figure 4.5 d-f, j-i). Even under scenarios in which the pooled data suggested there was no association expected between evolutionary age and range size (REM 1), range size did vary with the ages of species in at least 30% of individual clades (Figure 4.5a-c) .

The frequency with which each model is supported in the observed and simulated data show that some regions of parameter space are more able to reproduce the observed trends (Figure 4.5c) than others (Figure 4.5d). Generally a better match is achieved when σ^2 is high (Figure 4.5 c,f,i,l) compared to where it is low (Figure 4.5 a,d,g,j). Overall, however, the correspondence between the observed and simulated data is striking (Figure 4.5). The simulated data predicts that in most clades range size should be independent of evolutionary age (REM 1), but that a high proportion of clades should also show an increase in range size with evolutionary age (REM 2). Other models are then sometimes represented, but not very frequently. This is precisely the pattern we find amongst the observed clades (Figure 4.1).

Figure 4.5. On the following page. Comparison of the frequency of range evolution models (REM's) observed in birds and mammals (red lines) to that occurring in simulations in which range size has evolved at random. Black dots and lines are the mean and 95% confidence intervals for the number of times each model was selected from 100 random draws of 65 clades from the set of 5000 replicate simulation runs. Shown are the effects of rate of range evolution (σ^2), range split asymmetry (β) and dependence of speciation probability on range size ($rs\lambda$). Going from left to right shows the effect of increasing (σ^2) while keeping speciation parameters fixed. Going from top to bottom shows the effects of varying the speciation parameters while keeping σ^2 fixed. a-c) ($\beta = 10$, $rs\lambda = +$), d-f ($\beta = 1$, $rs\lambda = 0$), g-i ($\beta = 10$, $rs\lambda = +$), j-l ($\beta = 1$, $rs\lambda = +$). These parameter combinations are a representative subset of the full range of parameters values investigated (see Table 4.2). REM models were fitted using standard linear and polynomial regressions with the best model selected as the model with the lowest AIC (see Table 4.2 for REM curve shapes).


σ2 = 1 x 10^4
σ2 = 1 x 10^8
σ2 = 2.25 x 10^10
a)
b)
c)
d)
e)
f)
g)
h)
i)
j)
k)
l)
Frequency
Range evolution model

4.5 Discussion

In almost half of the avian and mammalian clades examined in this study range size was dependent on evolutionary age. The shape of this relationship varied between clades, with cases of monotonic increases, monotonic declines and peaked relationships, in which maximum or minimum range sizes occurred amongst species of intermediate age. These patterns were present in relatively similar proportions when clades where analysed at the level of genus or order. These patterns could imply the occurrence of systematic trajectories in range size over evolutionary time (Jones et al. 2005; Paul et al. 2009; Ricklefs & Bermingham 1999; Webb & Gaston 2000). Indeed, it was based on this species-for-time comparison that Willis (1922) formulated his theory of "Age and Area" in which geographic ranges tend to expand through time. However, simulations show that such relationships between evolutionary age and range size among extant taxa are expected even if geographic ranges have no tendency to expand or contract through time due to the effects of speciation and extinction. Comparison of the observed and simulated clades shows that the observed patterns and largely consistent with geographic ranges of birds and mammals having evolved according to a random walk through time.

In the simulations, species with small geographic ranges rapidly become extinct compared to those with larger ranges simply due to stochastic fluctuations in range size. Because species with extensive distributions survive for longer, on average they will tend to be older than species with restricted ranges. This results in a positive relationship between range size and evolutionary age even if ranges have had no tendency to expand through time. While previous studies have interpreted this positive relationship as

evidence for range expansion (Paul et al. 2009; Webb & Gaston 2000), the results show that this pattern can also be caused by extinction alone. Given the evidence for high rates of extinction in the fossil record and the dependence of these rates on range size (Jablonski 1995; Jablonski 2008), extinction may be a more parsimonious explanation than range expansion.

In fact, the illusion of range expansion may not even depend on extinction. A positive relationship also arises if rates of speciation are independent of range size. This is because speciation is accompanied by the splitting of the geographic range into two daughter ranges each of which is smaller than the parent (Anderson & Evensen 1978; Waldron 2007). Species with large ranges will therefore tend to be those which have not recently speciated and are thus older. I did not simulate a model in which speciation probability declined with range size (Jablonski & Roy 2003). However, I expect that this would lead to an even steeper increase in range size with evolutionary age because here older species with large ranges would be less likely to speciate.

When the probability of speciation increases with range size, this can lead to a variety of relationships between range size and evolutionary age depending on the asymmetry of range division. When range division is highly asymmetric (e.g. following the colonisation of an island or microallopatry), one of the daughters receives the majority of the parent range thus maintaining the ancestral range size through time (Waldron 2007). In this case, species which currently have large ranges are likely to have undergone speciation only recently and so will therefore appear young. This results in a negative relationship between range size and evolutionary age. Only when extinction occurs at a rate that balances this negative trend would the expectation that range size is

independent of evolutionary age be valid. If range division is more equal then both daughters inherit range sizes much smaller than that of their parent. This tends to erode the signal of the positive relationship between range size and speciation probability and so can also lead to the expectation that range size is independent of evolutionary age. However, this is conditional on extinction rates being sufficiently low that they do not cause an upturn in range size with evolutionary age.

A negative relationship between range size and evolutionary age has often been interpreted as evidence of a "taxon cycle" model (Wilson 1961) in which ranges rapidly expand following speciation and then gradually decline to extinction (Jones et al. 2005; Ricklefs & Bermingham 1999; Webb & Gaston 2000). The results of the simulations show that a pattern mirroring the taxon cycle can also occur if a widespread species has produced many species with smaller ranges, each of which has a reduced chance of speciating but also a low probability of extinction. These conditions may in fact be most likely to occur on island archipelagos where taxon cycles have been most commonly invoked (Greenslade 1968; Ricklefs & Bermingham 1999; Ricklefs & Cox 1972; Wilson 1961). Here, a species from the mainland gives rise to a number of daughter species each endemic to an individual or small number of islands and these persist for long periods of time in isolation (Price 2008). These results suggest that a negative relationship between range size and evolutionary age need not imply taxon cycle like dynamics.

The simulations show that the conditions under which range size is expected to be independent of evolutionary age are limited, requiring particular combinations of extinction rates and speciation mode. On this basis our perception of the patterns observed across birds and mammals may be reversed. No longer do the examples of

correlations between range size and evolutionary age require special explanation, rather, it is the large number of cases where no relationship exists that seem remarkable. However, the stochasticity of the diversification process means that even in regions of parameter space where a trend between range size and evolutionary age is expected, the majority of clades will still exhibit no relationship between evolutionary age and range size.

That simulations of random range evolution can produce the variety of patterns observed in mammals and birds is in itself notable. However, a much stronger test of a departure from randomness is to examine the relative frequency with which different patterns are predicted under the simulations compared to the observed data (Phillimore et al. 2008). Across the 65 genera I studied, range size was correlated with evolutionary age in slightly less than half of these. Of those showing a relationship, the most common pattern was for an increase in range size with evolutionary age, with other models occurring less frequently. Across large areas of parameter space the simulations mirror these observed patterns and in some cases the match between the observed and simulated results is quite striking. The number of observed clades exhibiting trends in range size with evolutionary age therefore does not appear to differ for that expected if ranges had evolved randomly through time.

4.6 Conclusion

The simulations developed here show that even when range size evolves randomly through time this often leads to correlations between evolutionary age and range size due

to the effects of speciation and extinction. Comparison of these expected patterns to those observed across real clades of birds and mammals shows that there is little evidence for ranges having undergone systematic changes through time. Instead the patterns appear to be consistent with a model in which range size evolution is largely a random process.

Chapter 5

Gene flow and the geometry of geographic ranges

5.1 Abstract

Theory predicts that the extent of gene flow amongst populations within a species should depend critically on the shape of the geographic range. Differences in the shapes of species' ranges could therefore provide a general explanation for the variation in the genetic cohesion and rates of speciation across taxa. Here I compile a geographical database of population F_{ST} estimates for species of birds, mammals and amphibians and test whether range geometry can account for the differences amongst species in the extent of neutral genetic differentiation. I find that, within a given species, accounting for the shape of the geographic range connecting populations improves predictions of their relative genetic differentiation compared to distance metrics which ignore range shape. However, the overall extent of genetic differentiation exhibited by a species was unrelated to the shape of its geographic range. The results suggest that, while the geometry of species' distributions can restrict gene flow between populations, range shape is unlikely to provide a general explanation for the observed differences in the degree of genetic cohesion across taxa.

5.2 Introduction

Populations within species are seldom entirely genetically independent of one another, but are instead linked by gene flow to other populations across the geographic range (Mayr 1963). However, the genetic cohesion of populations varies dramatically across species (Ehrlich & Raven 1970; Morjan & Rieseberg 2004). By limiting the degree of local adaptation (Antonovics 1976), the cohesive effects of gene flow can determine the potential for geographic range expansion (Kirkpatrick & Barton 1997), niche evolution (Holt & Gomulkiewicz 1997), the dynamics of species interactions (Thompson 2005) and ultimately the opportunity for speciation (Endler 1977; Mayr 1963). Understanding the causes of variation in gene flow across species therefore underlies many of the most fundamental questions in evolutionary biology.

Because of the limited spatial scale of organism dispersal, gene flow between populations tends to decline with their degree of spatial separation (Jenkins et al. 2010; Wright 1943 but see Finlay 2002). This leads to the well known pattern of isolation by distance, in which the genetic differentiation between populations increases across space (Wright 1943). The rate of decay in genetic similarity with distance is dependent on the scale of organism dispersal: strong disperses exhibit high gene flow over larger distances, and thus less genetic differentiation, than weak dispersers (Bohonak 1999; Burney & Brumfield 2009; Morjan & Rieseberg 2004; Peterson & Denno 1998). A combination of large geographic ranges and low vagility is therefore expected to provide the greatest opportunities for genetic differentiation (Morjan & Rieseberg 2004), population

divergence (Belliure et al. 2000; Phillimore et al. 2007) and speciation (Endler 1977; Kisel & Barraclough 2010; Losos & Parent 2009).

In addition to geographic scale, the genetic cohesion of a species should depend on the shape of its geographic range and the resulting geometrical arrangement of populations (Wright 1943). When species are distributed across a two-dimensional landscape (Figure 5.1a) gene flow can occur in all directions and is expected to decline with the logarithm of the distance separating populations (Slatkin 1993). In contrast, when species are distributed in a linear habitat (Figure 5.1b), the connectivity amongst populations is reduced and gene flow is expected to decline more precipitously across space, in proportion to the absolute distance separating populations (Endler 1977; Rousset 1997; Slatkin 1993; Wright 1943). Mathematical models suggest that this reduction in gene flow should give rise to faster rates of speciation in taxa possessing linear ranges (Gavrilets et al. 2000)

Species differ dramatically in the shapes of their geographic ranges (Graves 1988; Rapoport 1982; Ruggiero 2001; Ruggiero et al. 1998) (Figure 5.2). In birds for instance, species living along coastlines, rivers or tropical mountain chains approximate one-dimensional ranges (e.g. *Campylorhynchus rufinucha* Figure 5.2), while those occurring in the continental interiors and lowlands have more two-dimensional distributions (e.g. *Andropadus virens* Figure 5.2) (Chapter 3). Even here, however, range shape varies widely according to the particular configuration of habitats and environmental gradients (Chapter 3). The most striking contrast in range shape occurs between the Andes and the adjacent Amazon basin: while species occupying the lowlands have almost circular

distributions those restricted to the narrow bands of habitat along the mountain chain often have ranges that are over 300 times long as they are wide (Graves 1988).

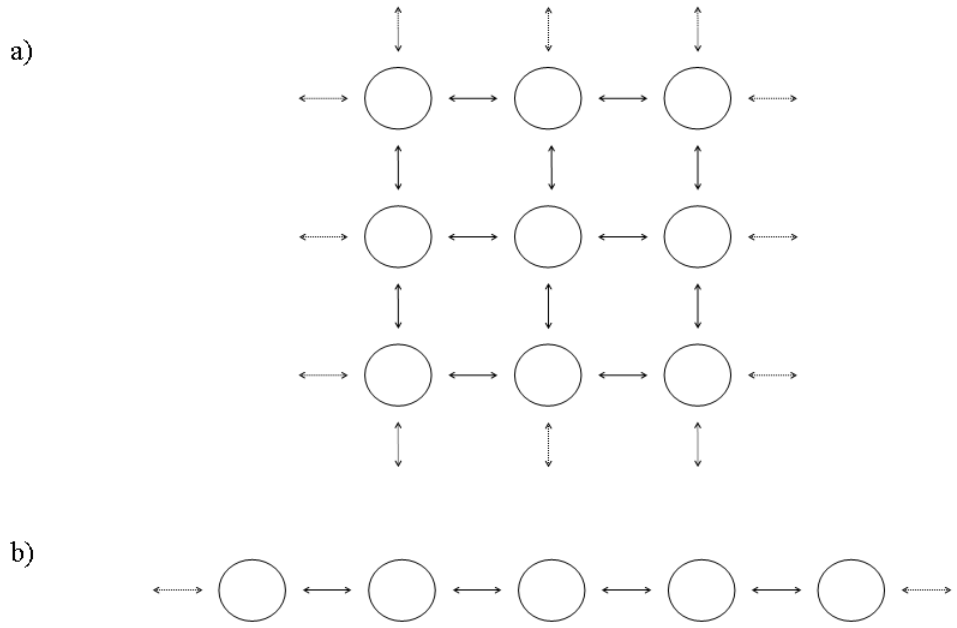


Figure 5.1. Idealised range geometries showing populations (circles) linked by gene flow (arrows) in a) a two-dimensional array and b) a one-dimensional/linear sequence.

Given this striking geographical variation, the idea that range shape could explain differences amongst species in genetic cohesion and the rate of speciation is compelling. Indeed, reduced range dimensionality has been put forward as an explanation for a number of well known radiations, including Cichlid fish in the African Great Lakes (Gavrilets & Losos 2009), Lake Baikal Gammarids (Brooks 1950) and Andean birds (Graves 1988). However, despite this substantial body of theory and its potential implications for broad scale patterns in diversity, the role of range shape in explaining differences in genetic cohesion across species remains almost completely untested.

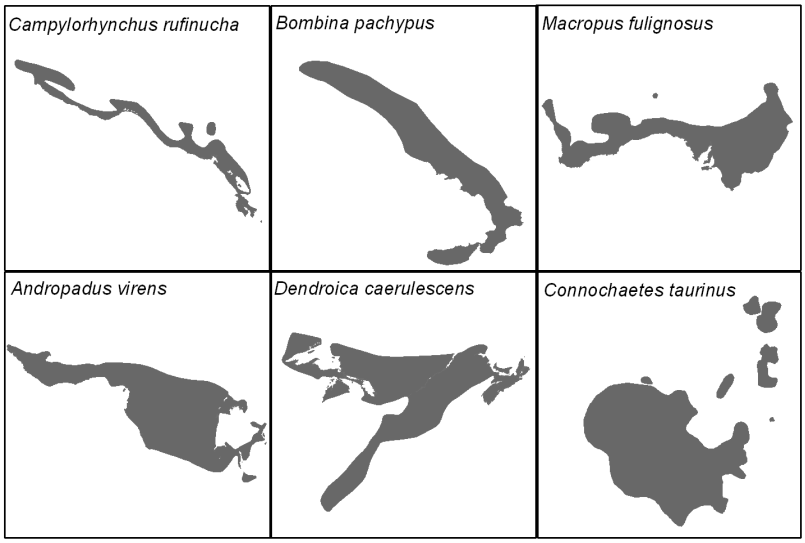


Figure 5.2. Variation in geographic range shape observed across species. Geographic ranges have been scaled to equal dimensions and projected in an Albers equal area projection centred on the geographic range of each species. Species are from the F_{ST} database presented here.

If linear ranges reduce gene flow then this should be evident as both a higher rate of isolation by distance and higher overall levels of differentiation amongst populations compared to in two-dimensional ranges (Endler 1977; Rousset 1997; Slatkin 1993; Wright 1943). McRae and Beier (2007) recently developed an elegant method, based on electrical circuit theory, for quantifying the shape of the habitat connecting populations across a species' range. For two selected species they showed that this metric improved prediction of the relative genetic differentiation amongst populations compared to distance alone (Lee-Yaw et al. 2009; McRae & Beier 2007). Whether range shape can also explain differences in genetic differentiation amongst species was not examined.

Here, I conduct a meta-analysis of the effects of range shape on genetic differentiation across a range of vertebrate species. As a measure of genetic differentiation, I compile a geographical database of pairwise-population F_{ST} estimates from the literature. I then use circuit theory to quantify the shape of the geographic range connecting sampled populations (McRae & Beier 2007) and analyse the effects of range shape on genetic differentiation at two hierarchical levels. First, within each species I examine whether variation across space in the shape of the range can explain the relative extent of genetic differentiation amongst populations (McRae & Beier 2007). Second, I examine whether differences amongst species in their overall levels of genetic differentiation can be explained by differences in the shapes of their ranges. In both the within- and across-species analyses, I examine the effects of range shape alongside other biological traits and methodological factors that are thought to influence genetic differentiation. Because closely related species may share similar traits, I also assess the effects of range shape on genetic differentiation using phylogenetic comparative methods.

5.3 Methods

5.3.1 Population F_{ST} estimates

F_{ST} provides a widely used measure of genetic differentiation, increasing from 0 towards 1 as the variance in allele frequencies amongst populations increases relative to that within populations (Wright 1943). I searched the literature for studies reporting pairwise-population F_{ST} estimates (or F_{ST} analogues) across multiple geo-referenced populations. I

did not consider studies reporting single F_{ST} values because populations are rarely sampled from throughout a species' distribution and it is important to account for this when testing the effects of range shape (see below). I also restricted my search to species of birds, mammals and amphibians, for which complete global vector maps of native breeding ranges are readily available (Orme et al. 2005; Schipper et al. 2008; Stuart et al. 2004).

Using F_{ST} as an indirect measure of gene flow has to be treated with caution because the underlying 'island model' makes a number of simplifying assumptions, including that; there is no selection or mutation, gene flow and drift are in equilibrium and, there is no spatial structure (Bossart & Prowell 1998; Whitlock & McCauley 1999). For transparency I therefore use the original F_{ST} values in the analysis rather than converting these to estimates of gene flow.

5.3.2 Geographic data

The application of circuit theory to calculate the shape of the range connecting populations requires gridded range maps (McRae & Beier 2007). For each species I therefore extracted the vector map of its native breeding distribution onto a rectangular grid of 25km resolution. Cells intersecting the vector range were recorded as present and those not intersecting the range were recorded as absent. I chose this spatial scale in order to maximise the number of populations in the analysis (see below) and reduce the overestimation of species' ranges while also maintaining computational efficiency. To avoid edge effects arising from the boundaries of the grid, the bounding box of each species' grid was extended by 500 km beyond the limits of the species' range (Koen et al.

2010). Prior to gridding, I projected each range onto an Albers equal-area projection centred on the geographic range of that species in order to minimise distortion in range shape arising from global projections. For species spanning multiple continents, the projection was centred over the continental range in which populations were sampled.

For each species, I mapped the sampled populations to cells on the grid using either the geographic coordinates reported in the study or from online gazetteers when the name of the nearest locality was provided. I excluded sampled populations where the location was ambiguous or did not overlap the geographic range of the species. If multiple populations had been sampled within a single cell, the population with the largest number of sampled individuals was retained. Where no information on sample size was available, the population retained was selected at random. I also excluded sampled populations that fell in disjunct range fragments, retaining only species where at least four populations were sampled within the same contiguous range fragment. Finally, I only retained those species where suitable populations had been sampled over a geographic distance of at least 200km, in order to exclude those studies focusing on genetic differentiation at landscape scales (Peterson & Denno 1998).

The number of suitable populations for each species ranged from 4 to 21 (median = 8). The majority of studies used microsatellite or mitochondrial DNA and so I excluded the few studies using allozymes, Amplified Fragment Length Polymorphism's and Random Amplification of Polymorphic DNA. This resulted in 554 populations from 60 species meeting my criteria (Appendix 4 Table S1). These species were relatively evenly distributed amongst taxonomic groups (birds=21, mammals=21, amphibians=18), and

geographically widespread, occurring on all continents except Antarctica (Appendix 4 Figure S1).

5.3.3 Measuring range shape

To quantify the shape of the range connecting sampled populations I used circuit theory implemented in the program Circuitscape v3.5.1 (McRae 2006). In this method, each cell on the grid is represented as a node within a graph, with each node connected to its 8 immediate neighbours by resistors. The resistance between any pair of nodes is calculated based on the length and number of all possible pathways connecting them in the graph (McRae 2006). Cells further apart have a greater resistance than those close together. For a given distance, cells connected by many pathways, such as in a two-dimensional landscape, will have a low resistance. In contrast, cells connected by few pathways, such as in a linear landscape, will have a high resistance (McRae 2006).

To separate the effects of distance and shape, two landscapes were used to calculate resistance values for each pair-wise combination of sampled populations. First, cells were assigned as unit resistors regardless of whether the cell was occupied by the species or not (Isotropic Resistance or IR). Resistance is then calculated using all possible pathways across the grid. This therefore assumes that gene flow is not constrained by the shape of the geographic range and is equivalent to the log-transformed great-circle distance between populations (McRae 2006) (Figure 5.3a). Second, cells unoccupied by the species were excluded (assigned as infinite resistors) so that only those pathways occurring through the geographic range were used when calculating resistance (McRae & Beier 2007). This assumes that gene flow is entirely constrained by the shape of the range

(Shape Resistance or SR) (Figure 5.3b) (McRae 2006). Finally, I also calculated the length of the single shortest pathway passing entirely through the geographic range, the Least Cost Path (LCP) (Figure 5.3c). The LCP takes account of the greater distance incurred by restricting pathways to occur through the range but does not account for the number of pathways connecting populations (McRae 2006).

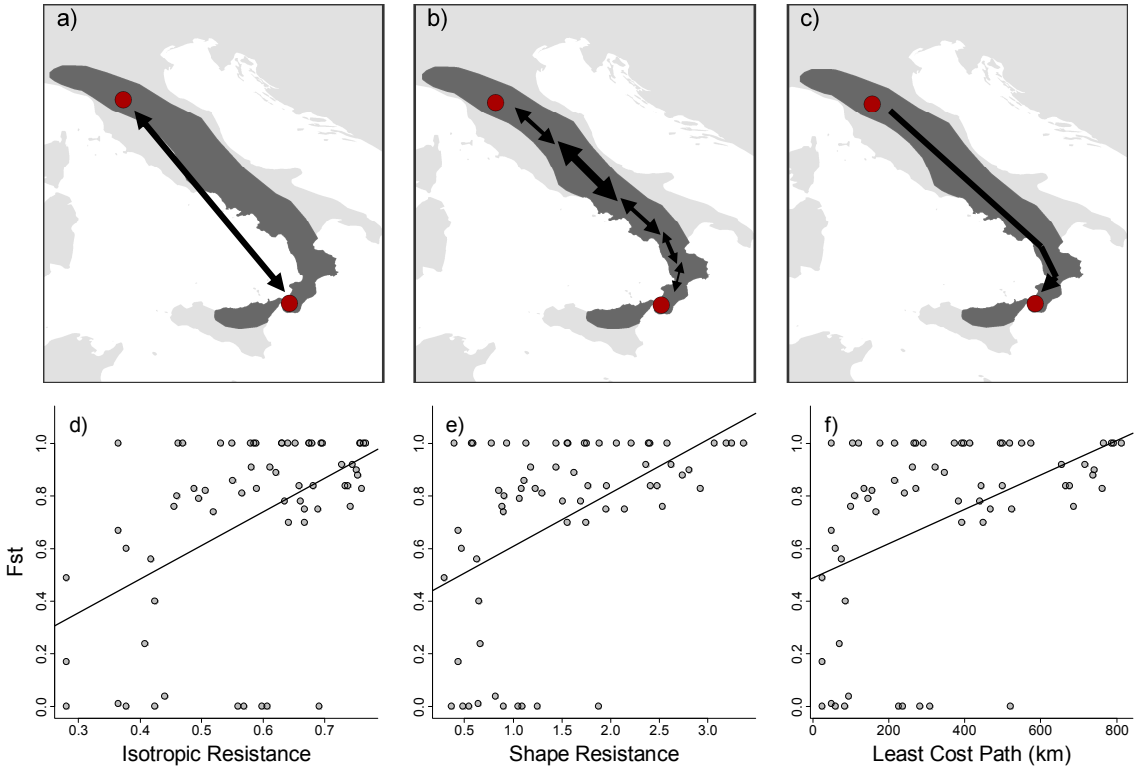


Figure 5.3. Measurement of resistance and OLS regressions against F_{ST} for the Appennine Yellow-bellied Toad (*Bombina pachypus*) under a, d) Isotropic Resistance (IR), b, e), Shape Resistance (SR) c, f) Least cost Path (LCP). Red dots are examples of two populations between which F_{ST} has been estimated with arrows representing how resistance between populations is calculated.

5.3.4 Phylogeny

For the species in the F_{ST} dataset I constructed a phylogenetic tree for each vertebrate class according to a relaxed clock Bayesian method in BEAST v1.5.4 (Drummond & Rambaut 2007). Sequences for 3 mitochondrial genes (Cytb, Coi, ND2) and 1 nuclear gene (Rag1) were downloaded from GenBank using GENEIOUS (Drummond et al. 2006) and aligned by eye in MEGA v4 (Kumar et al. 2004). Because Rag1 was only available for some of the species in the F_{ST} dataset (n=25) I included congeneric or confamilial representatives for which adequate sequence data were available. These guide species were then pruned from the final tree before further analysis (Appendix 4 Table S2). No sequences were available for *Litoria pearsoniana*, which was therefore represented in the tree by its congener, *Litoria caerulea*. For each class, I included an appropriate outgroup to root the tree (Birds: *Struthio camelus*; Mammals: *Ornithorhynchus anatinus*; Amphibians: *Boulengerula boulengeri*).

Within BEAST (Drummond & Rambaut 2007), I used a general time-reversible substitution model with four gamma categories and separate partitions for mitochondrial and nuclear genes. I assumed that variation in rates of molecular evolution amongst branches were log-normally distributed and used a Yule prior on branching times. For each class, I conducted a single run of 50 million generations sampling every 5000 generations. I discarded the first 1000 trees to give a sample of 9000 trees, which were combined to give a maximum credibility tree for each class. Tree log files were assessed using *Tracer* (Rambaut & Drummond 2007) and estimated sample sizes for the general time-reversible model parameters were almost always >200. The three class level trees were then joined using estimates of the date of splitting events between amphibians and

amniotes (350 Mya) and mammals and birds (320 Mya) obtained from Alfaro (2009). The species included in the phylogenetic trees, GenBank sequence accession numbers and the final inter-class tree are provided in Appendix 4 Table S2 and Figure S2.

5.3.5 Additional predictors of variation in F_{ST}

In addition to effects of range shape, gene flow may also vary with species biological traits or methodological differences in the measurement of F_{ST}. I therefore included seven additional explanatory variables in the analysis. Variables exhibiting positive skew were log-transformed prior to analysis (Freckleton 2000).

i) *Variance in Range Shape*. Regardless of the absolute width of the range connecting populations, if this is constant amongst populations then the relative ability of the resistance metrics to explain variation in F_{ST} will not differ (McRae 2006; McRae & Beier 2007). When analysing F_{ST} amongst populations within species, the effects of range shape are therefore expected to increase with the variation in the width of the range. In the within species analysis, the variance in SR across population pairs was included a predictor variable.

ii) *Genetic Marker*. The smaller effective population sizes arising from maternal inheritance of mitochondrial genes is expected to result in greater levels of genetic drift and thus F_{ST} estimates (Zink & Barrowclough 2008). Mitochondrial genes will also approach migration drift-equilibrium more rapidly than nuclear genes and so are more likely to detect the effects of

current range configuration than nuclear genes (Zink & Barrowclough 2008). I therefore included the identity of the genetic marker (mitochondrial or microsatellite) as a two-level factor in the analysis.

iii) *Sample Size*. Species in which a larger number of populations have been sampled should have more reliable F_{ST} estimates and may be more likely to detect any effect of range shape on genetic differentiation (Jenkins et al. 2010).

iv) *Geographic Extent*. The geographic distance over which populations are sampled is expected to determine the overall genetic differentiation (Bohonak 1999), the relative importance of gene flow and drift (Hutchison & Templeton 1999), and whether the habitat connecting populations is effectively one or two dimensional (Rousset 1997). For each species, I therefore calculated the maximum great circle distance separating sampled populations as a measure of geographic extent.

v) *Latitude*. The geographic ranges of species at high latitudes have shifted repeatedly in response to past changes in climate (Dynesius & Jansson 2000; Hewitt 2000). This could lead to weaker patterns of genetic differentiation (Martin & McKay 2004) and may reduce the match between current range shape and population genetic structure. I therefore recorded the absolute latitudinal midpoint of the focal populations for each species.

vi) *Dispersal Mode*. Species with strong dispersal abilities will exhibit greater gene flow amongst populations (Bohonak 1999; Burney & Brumfield 2009; Slatkin & Maddison 1990). Dispersal distances are not widely available for the

species in this study and so I categorised species as either volant (birds and bats) or non volant (amphibians and all other mammals) (Alexander 2002).

vii) *Body Mass*. For active dispersers, movement distances scale positively with body size (Jenkins et al. 2007; Sutherland et al. 2000) while population density declines (Damuth 1981). This should lead to both higher gene flow and drift in large bodied species, altering the shape of the isolation by resistance relationship (Hutchison & Templeton 1999). I collected species mean body mass (g) values from a variety of sources (Appendix 4 Table S1). Species values were obtained by calculating the mean across males and females, weighted by sample size. For some species of amphibians, body mass data was not available. In these cases, I estimated body mass from the snout-vent-length (SVL) using family-specific conversion factors (Deichmann et al. 2008).

5.3.6 Within species analysis

I assessed whether variation in the shape of the range connecting populations influenced the relative extent of gene flow between them by comparing the ability of each resistance metric to predict patterns of neutral genetic differentiation (McRae & Beier 2007) (Figure 5.3d-f). For each species, I obtained the r^2 from the ordinary least squares regression (OLS) of pairwise F_{ST} estimates against each resistance metric (Figure 5.3d-f). I highlight that because each SR value is equal to or greater than its corresponding IR value, a higher r^2 under the SR metric indicates that linear habitats are associated with greater genetic differentiation. If there was less genetic differentiation in linear habitats this would result in a lower r^2 under the SR metric.

The significance of the OLS slopes were calculated using Mantel tests with 10,000 permutations. I then modelled r^2 as a function of the type of resistance metric both alone, and in multi predictor models, with the seven additional explanatory variables included as both main fixed effects and as interactions with resistance metric. Because the three r^2 values for each species will be correlated, I included species identity as a random effect. I repeated this model fitting including phylogenetic covariance between species as a random effect to capture similarity due to shared evolutionary history (Hadfield & Nakagawa 2010).

In order to fit these models within the same analytical framework, I used generalised linear mixed effect models, fitted using Bayesian Markov Chain Monte Carlo methods in the program R (MCMCglmm: (Hadfield & Nakagawa 2010)). For all models, I set flat non-informative priors with a low degree of belief across all variables. Models were run for 100,000 generations with the first 10,000 generations discarded as burn-in and then sampled every twenty generations to generate posterior distributions. Model fit was assessed using the Deviance Information Criterion (DIC), with lower values indicating a better fit. Multi predictor models were simplified to produce a minimum adequate model (MAM) by stepwise backwards elimination, removing those terms that resulted in the greatest decrease in DIC. I stopped removing variables when the removal of terms no longer resulted in a decline in DIC. In order to account for stochastic differences in the posterior distributions, I repeated model simplification steps five times and used the average change in model DIC to identify terms to be deleted.

5.3.7 Across species analysis

I then conducted a meta-analysis of the effects of range shape on the overall extent of genetic differentiation amongst species. Species wide measures of range shape (Chapter 3) are not appropriate because populations were seldom sampled from throughout the entire range of a species. I therefore calculated the proportional increase in resistance between the IR and SR metrics (SR/IR) for all pairs of populations for a species and use the median increase as a species level measure of range shape. Higher values of SR/IR indicate a more linear distribution and hence lower connectivity amongst populations.

In order to standardize the distance over which differentiation occurs and to assess the effect of range shape at different scales, I used the species level OLS regressions of F_{ST} and IR to predict the level of genetic differentiation at four scales (resistance values corresponding to 100km, 500km, 900km and 1300km)(Kisel & Barraclough 2010). I then tested whether differences between species in SR/IR predicted variation in these standardized F_{ST} values. The additional explanatory variables were included as both main effects and in interactions with SR/IR. I again used MCMCglmm to identify minimum adequate models using the process described above (Hadfield & Nakagawa 2010). In addition to random covariance effects introduced by phylogeny, the reliability of each standardised F_{ST} estimate will vary depending on the number and spatial distribution of populations sampled for that species. For instance, a species with a small number of closely spaced populations would produce less reliable estimates of genetic differentiation at large scales than a species with many sampled populations, some of which are separated by large distances. I accounted for this by including the standard

errors associated with each standardised F_{ST} estimate as a random effect in the models (Hadfield & Nakagawa 2010).

5.4 Results

5.4.1 Within species analysis

Almost half of the species examined exhibited a significant relationship between resistance and F_{ST}, with more spatially isolated populations being more genetically differentiated than populations close together (Figure 5.4). The percentage of significant relationships was similar across resistance metrics, being slightly higher when including the effects of range shape (SR) (48%) than either the IR (40%) or LCP (38%) metrics.

The ability of the resistance metrics to explain the variation in F_{ST} differed substantially across species (Figure 5.5). For instance, the SR metric accounted for over 90% of the variation within the Little Greenbul (*Andropadus virens*) but almost no variation within the Darked-eyed Junco (*Junco hyemalis*) ($r^2 = <1x10^{-6}$). Despite this large variation in explanatory power across species, the mixed effect models showed that the choice of resistance metric had a significant effect on the ability to explain the patterns of F_{ST} within each species. Overall, estimated r^2 values were significantly higher for the SR ($p=0.02$, Table 5.1, Figure 5.5) than the IR metric, while the IR metric and LCP did not differ in their explanatory power (Table 5.1). I note, however, that the increase in explanatory power associated with the SR metric was relatively small, increasing the average explained variance from 16% (IR) to 20% (SR). Nevertheless, the higher explanatory power of the SR metric indicates that for a given distance genetic

differentiation tends to be higher amongst populations connected by more linear habitats than those in more two-dimensional areas.

Multi predictor models highlighted a significant positive interaction between the SR metric and body size (Table 5.1). This shows that the higher explanatory power of the SR metric was driven by large bodied species. Although some terms are retained in the MAM by the DIC fitting procedure, there were no significant effects of latitude, sample size, geographic extent, genetic marker, dispersal mode or variance in range shape on the relative explanatory power of the resistance metrics (Table 5.1).

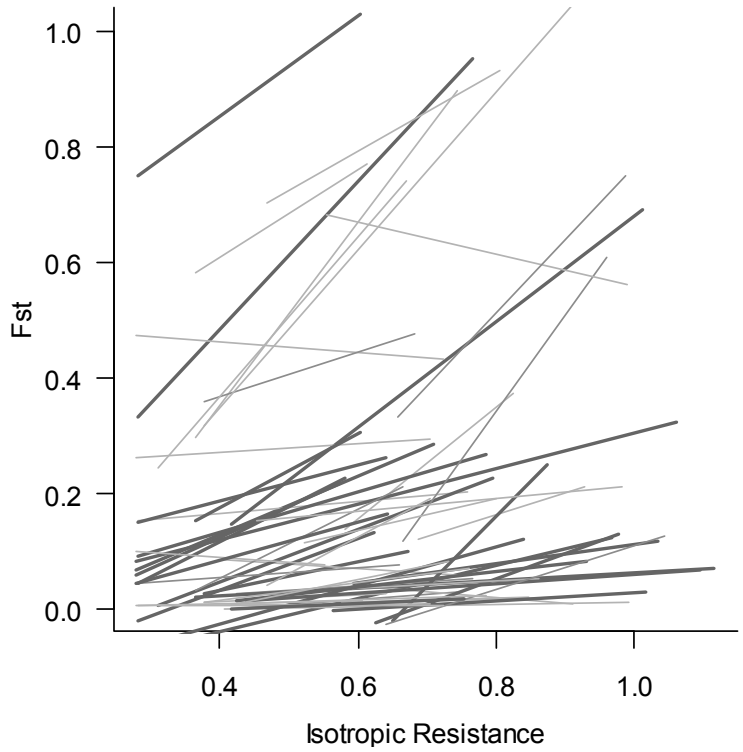


Figure 5.4. Isolation by Isotropic Resistance (IR) showing the OLS regression of IR against F_{ST} for each species. Line shading and weight indicates statistical significance of the slope according to a mantel test (thin light gray p>0.1; thin medium gray p < 0.1; thick dark gray p < 0.05).

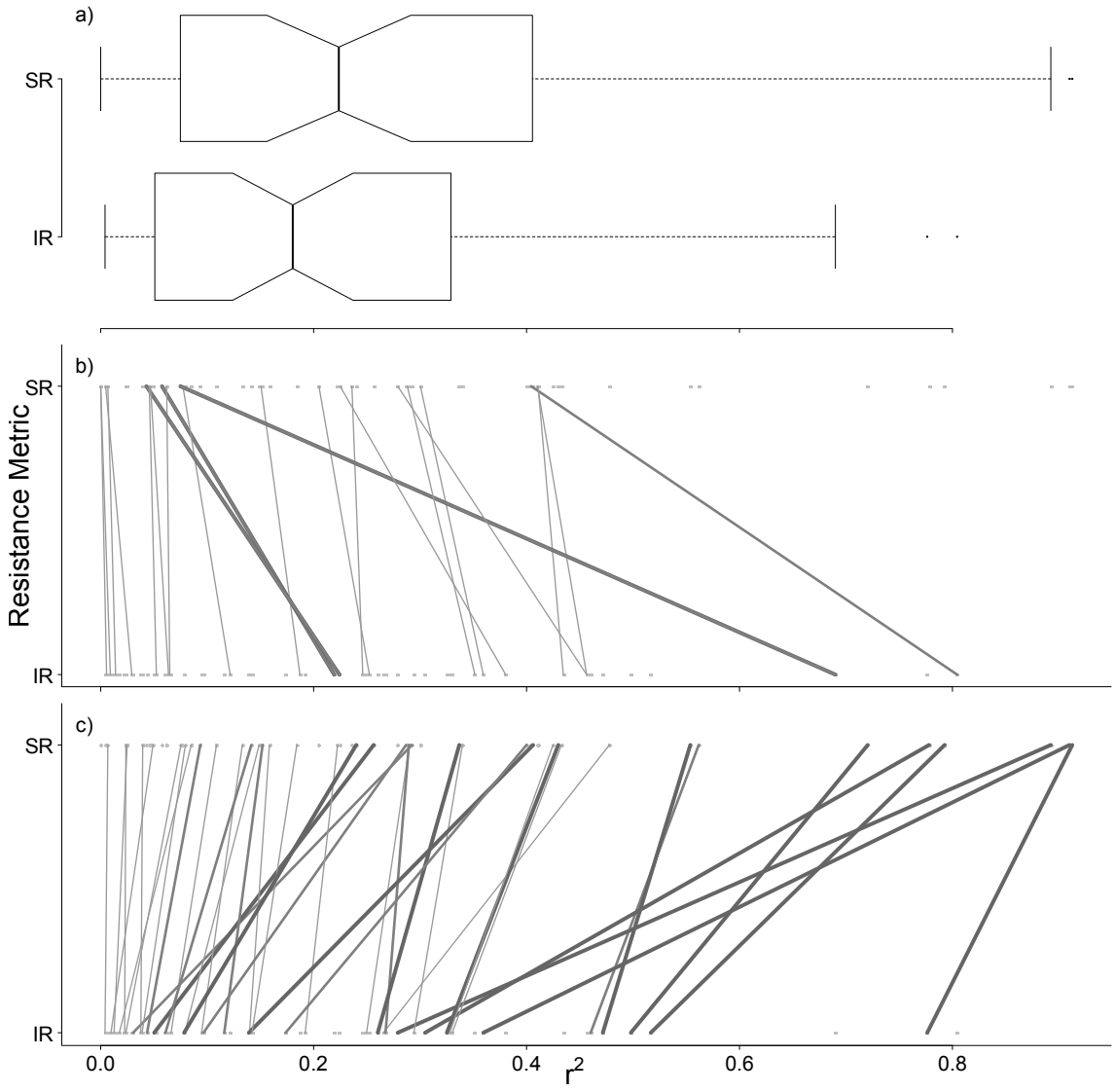


Figure 5.5. Explanatory power (r^2) of OLS models of resistance metric against F_{ST} for the Isotropic Resistance (IR) and Shape Resistance (SR) metrics a) box and whisker plot for all species, and b,c) differences in model explanatory power for individual species, in cases where IR outperforms SR (b) and where SR outperforms IR (c). Line shading and weight indicates statistical significance of difference in explanatory power of resistance metrics according to a partial mantel test (thin light gray $p>0.1$; thin medium gray $p < 0.1$; thick dark gray $p < 0.05$).

Resistance Metric Alone (DIC = -1088.468)					
Fixed Terms		Posterior mean	1-95% CI	u-95%	P
		0.0414	**0.0355**	**0.0478**	**<0.001**
Resistance metric	LCP	0.0010	-0.0028	0.0047	0.6000
	SR	**0.0045**	**0.0006**	**0.0081**	**0.0204**
Resistance Metric MAM (DIC = -1092.480)					
		0.0655	**0.0372**	**0.0948**	**0.0002**
Resistance metric	LCP	0.0011	-0.0053	0.0072	0.7298
	SR	-0.0004	-0.0062	0.0058	0.8924
Dispersal Mode		0.0101	-0.0013	0.0218	0.0924
Body Mass		0.0009	-0.0009	0.0029	0.3484
Marker		-0.0126	-0.0248	0.0008	0.0600
Shape Index(var)		**0.0031**	**0.0006**	**0.0057**	**0.0156**
N		-0.0113	-0.0235	0.0015	0.0707
	LCP x Body Mass	0.0000	-0.0013	0.0011	0.9502
	SR x Body Mass	**0.0012**	**0.0000**	**0.0023**	**0.0413**

Table 5.1. The effects of resistance metric on IBR explanatory power (r^2). Results are from the MCMCglmm mixed effects model without phylogeny. Resistance metric is a categorical variable with three levels; Isotropic Resistance (IR), Least Cost Path (LCP) and Shape Resistance (SR). Results are presented as contrasts with IR set as the baseline. Dispersal mode and Marker are also categorical variables with "Volant" and "microsatellite" set as the baseline respectively. r^2 values were arc-sine transformed. Body mass (g), N, and Shape Index (var) are log-transformed. Significant effects at the 10% level are shaded grey. Significant effects at the 5% level are highlighted in bold.

5.4.2 Across species analysis

The predictors of neutral genetic differentiation between species were largely consistent across geographic scales, with the non-phylogenetic models consistently out-performing those including phylogeny. I therefore only present the results from the non-phylogenetic analysis at the 500km scale (DIC= -256) (Table 5.2). Results from the phylogenetic models and at other geographic scales are given in Appendix 4 Table S3. The MAM retained a number of significant predictor variables as main effects. F_{ST} values estimated from mitochondria were significantly higher than those estimated from microsatellites and non-volant organisms had higher F_{ST} values than volant organisms (Table 5.2). There was also a significant, albeit weak decline in F_{ST} with increasing latitude (Table 5.2). A number of significant interactions were also retained in the MAM. F_{st} estimates associated with mitochondrial markers and non-volant organisms were significantly lower for large compared to small bodied organisms. F_{ST} estimates from mitochondrial markers were also significantly reduced at high latitudes (Table 5.2). I note that in none of the models was range shape retained in the MAM either as a main effect or interaction term (Table 5.2; Appendix 4 Table S3).

Fixed Terms		Posterior mean	1-95% CI	u-95%	P
		0.082	-0.008	0.169	0.073
Marker		**1.170**	**0.788**	**1.540**	**0.000**
Latitude		**-0.002**	**-0.004**	**0.000**	**0.049**
Dispersal Mode		**0.221**	**0.095**	**0.344**	**0.001**
Body Mass		-0.011	-0.030	0.010	0.279
	Mitochondria x Latitude	**-0.022**	**-0.029**	**-0.015**	**0.000**
	Mitochondria x Body Mass	**-0.051**	**-0.082**	**-0.018**	**0.002**
	Latitude x Non-volant	-0.002	-0.004	0.001	0.156
	Latitude x Body Mass	0.000	0.000	0.001	0.106
	Dispersal Mode x Body Mass	**-0.016**	**-0.032**	**-0.002**	**0.035**

Table 5.2. MAM of the predictors of species F_{ST}. Species' F_{ST}'s were estimated from the OLS regression of F_{ST} against IR at a resistance value equivalent to 500km. Dispersal mode and Marker are categorical variables with "Volant" and "microsatellite" set as the baseline respectively. Body mass (g) is log-transformed. Significant effects at the 10% level are shaded grey. Significant effects at the 5% level are highlighted in bold.

5.5 Discussion

In this study I investigated the role of range shape in explaining variation in the genetic cohesion of species. Using a geographical database of F_{ST} estimates I analysed the effects of range shape at two hierarchical levels; the relative differentiation of populations within species, and the variation in genetic differentiation across species. I found that, within species, accounting for the shape of the geographic range connecting populations

improved predictions of genetic differentiation compared to simple distance metrics. For a given distance, populations connected by linear habitats were more differentiated than those in two-dimensional habitats. I also found that these effects were dependent on body size, with range shape having a greater effect amongst large bodied species. However, in contrast to the within species analysis, variation in the overall level of genetic differentiation between species could not be explained by differences in the shape of their ranges. Instead, having accounted for geographic scale and the genetic marker used to estimate F_{ST}, variation in genetic differentiation was driven by ecological traits, including dispersal mode and body size.

In almost half of the species analysed, there was a significant pattern of isolation by distance, whereby populations further apart were more genetically differentiated than those occurring in close proximity to one another (Wright 1943). This suggests that in many species gene flow and drift were approximately in equilibrium (Slatkin 1993). In addition to the effects of distance, genetic differentiation was higher amongst populations occurring in linear sections of the range compared to those in more two-dimensional areas. The results of the within species analysis therefore support the predictions of classical population genetic theory, that the lower connectivity of linear habitats leads to a reduction in gene flow between populations (Kimura & Weiss 1964; McRae & Beier 2007; Rousset 1997; Wright 1943)

The results also suggest that these effects of range shape on gene flow are dependent on body mass. While narrow habitats were associated with greater genetic differentiation in large bodied organisms, the width of the habitat had less of an effect for small organisms. Although the reason for this is uncertain, one explanation may be

related to the scale at which organisms recognise and respond to variation in the environment (Hutchinson & MacArthur 1959). Specifically, connectivity amongst populations of small organisms may be more dependent on landscape scale habitat features than the course scales captured using simple extent of occurrence maps (Anderson et al. 2010; Cushman & Landguth 2010).

Despite finding evidence for the effects of range shape within species, differences in the extent of genetic differentiation across species were unrelated to the shapes of their geographic ranges. There was no evidence that species with more linear distributions had higher levels of genetic divergence than species with more two-dimensional distributions. This was true even after accounting for methodological differences between studies and species-specific differences in ecology, and held regardless of the spatial scale at which genetic differentiation was estimated. This finding therefore fails to support the prediction of population genetic theory, that gene flow is reduced along linear ranges (Kimura & Weiss 1964; Rousset 1997; Wright 1943)

What could account for the differing outcomes of the intra- and inter-specific analysis? One possibility is that the effects of range shape could have been missed by the inter-specific analysis, if F_{ST} is not providing a reliable index of gene flow amongst populations (Whitlock & McCauley 1999). However, a number of other biological variables were identified as important correlates of genetic differentiation. For instance, genetic differentiation was higher for non-flying organisms, especially those with small body size, as would be expected if shorter dispersal distances are associated with lower levels of gene flow (Alexander, 2002; Sutherland et al. 2000; Bohonak, 1999; Peterson &

Denno, 1998). These biologically intuitive results suggest that F_{ST} is providing a reliable index of gene flow and that this is unlikely to account for the differences in the results.

An alternative explanation is that the effects of range shape on genetic differentiation were overwhelmed by other factors which are controlled for when looking at the patterns within species. For instance, F_{ST} estimates were significantly higher when using mitochondrial rather than nuclear genes (Zink & Barrowclough 2008). However, even having statistically accounted for these factors in the analysis, range shape was unrelated to genetic differentiation. It is possible that the inclusion of additional variables (e.g. habitat generalism, trophic level) could identify particular conditions where range shape does influence genetic differentiation. Nevertheless, this would not alter the conclusion that range shape does not appear to provide a general explanation for the variation in genetic differentiation across species.

I suggest that the most likely explanation for the mis-match in findings of the within and across species analysis relates to the dynamism of species' ranges. While variation in habitat geometry within a species may start to lead to differences in gene flow amongst populations, the shape of a species' range may be too ephemeral a property for this to accumulate into differences in genetic differentiation across species (Futuyma 1987; Jansson & Dynesius 2002; Losos & Glor 2003). Because species' ranges are strongly shaped by underlying climatic gradients (see Chapter 3), changes in these environmental conditions will lead to repeated alterations in the configuration of species' distributions. Species which currently have linear distributions may recently have had more two-dimensional ranges and vice versa (e.g. Aleixo 2006). Only in geographical settings where range shape is maintained through time (e.g. when range boundaries are

set by geological features such as rivers or coastlines), could this lead to consistent variation in the extent of genetic differentiation across taxa.

Through its effects on gene flow, range shape has been put forward as an explanation for differences in the rate of speciation across taxa and geographic regions (Brooks 1950; Gavrilets et al. 2000; Gavrilets & Losos 2009; Graves 1988). However, testing the effects of geographic ranges on speciation is difficult because the reciprocal feedback between ranges and speciation can confound standard comparative analyses (see Chapter 2). For instance, if species with linear ranges are prone to speciation then their geographic ranges may rapidly become broken up into a chain of allospecies, each with a more compact distribution. This could lead to the erroneous conclusion that species with compact ranges have higher rates of speciation. An alternative approach, and that taken here, is to analyse the effects of range shape on the processes underlying speciation.

In this study I found no evidence for greater genetic differentiation in species with more linear ranges casting doubt on the idea that range shape can explain differences in genetic cohesion and rates of speciation across taxa. If linear ranges do accelerate speciation then a more likely mechanism may be by increasing the rate at which populations become geographically isolated (Rosenzweig 1978; Chapter 2). There is some evidence that morphological divergence is higher in species with linear ranges (Graves 1988; Rapoport 1982). The results of this study suggest that this is more likely to arise by secondary contact of subspecies following a period of allopatry, rather than differences in the rate of divergence within continuous populations.

5.6 Conclusion

According to theory, gene flow should be reduced along linear geographic ranges, and this should lead to greater genetic differentiation. The results of this meta-analysis provide some support for this idea, showing that the relative genetic differentiation of populations within a species is partly attributable to the shape of the intervening habitat. However, the variation in overall genetic differentiation between species cannot be explained by differences in the shapes of their ranges. Range shape is therefore unlikely to provide a general explanation for the variation in the genetic cohesion of species.

Chapter 6

General discussion

6.1 The role of geography in species diversification

In this thesis I examined the role of geographic ranges in species diversification. While geography has long held a central position in the theory of speciation (Mayr 1942; 1963), how geographic ranges influence patterns of diversification have not been thoroughly explored. Most hypotheses invoking the effects of species' ranges are verbal and their underlying assumptions have rarely been tested (Diamond 1973; Dynesius & Jansson 2000; Price 2008; Rosenzweig 1995). In the General Introduction (Chapter 1) I highlighted four unresolved questions regarding the role of geographic ranges in diversification (Section 1.5). First, how does the interaction between range size and speciation affect the dynamics of species radiations? Second, what determines the limits to species' distributions? Third, how do geographic ranges evolve through time? And finally, do the shapes of species' ranges determine the potential for speciation?

6.1.1 Geographic speciation and the dynamics of diversification

In Chapter 2, I developed a geographical model of cladogenesis and used this to explore the phylogenetic patterns arising from geographic speciation. I showed that incorporating

this geographical context has a profound effect on the dynamics of diversification. For instance, depending on the particular combination of parameters, the model predicts both declining and accelerating rates of diversification and both highly balanced and unbalanced trees. These patterns arise because when the process of speciation is accompanied by the splitting of the geographic range, this alters both the absolute and relative chances of future speciation and/or extinction amongst the descendent lineages. As a result, even though the extrinsic events driving speciation (e.g. barrier formation) or extinction (e.g. range size fluctuations) may occur randomly through time this leads to 'non-random' patterns of diversification.

One important implication of these results is that they suggest that the traditional ecological niche based explanations for variation in diversification may need to be re-assessed. For instance, a pattern of tree imbalance is often interpreted as the result of variation in traits or environments amongst species promoting differences in speciation and/or extinction (Guyer & Slowinski 1993; Mooers & Heard 1997; Slowinski & Guyer 1993). But this pattern can also arise if speciation has occurred via peripatry (Chapter 2) because the asymmetry in daughter species' ranges arising from this process generates asymmetries in the rate of diversification (Chan & Moore 1999; Rogers 1996). This geographical explanation for variation in diversification rates may be particularly attractive at low taxonomic levels where trees can be highly unbalanced despite ecological similarity amongst species (Phillimore & Price 2008; Rundell & Price 2009).

Slowdowns in the rate of diversification are often explained in terms of adaptive radiation and niche filling (Harmon et al. 2003; Pinto et al. 2008; Schluter 2000 but see Purvis et al. 2009). Chapter 2 shows that a similar pattern could also arise if the rate at

which geographic ranges expand is insufficient to offset the division of ranges that occurs during speciation. Phillimore and Price (2008) have recently championed the role of range expansions in slowdowns, arguing that competition is the essential ingredient limiting geographic ranges (see also Rosenzweig 1995). However, geographic ranges could also be limited due to the persistence of the environmental gradients or barriers that initiated geographic isolation in the first place (Chapter 3). Phillimore and Price (2008) argued that these 'non-ecological' mechanisms are unlikely to explain the frequency of observed slowdowns because there is no reason to assume that the frequency of barriers was higher in the past. However, even if the frequency of barriers has remained constant through time, slowdowns can still arise because the chances of these barriers causing geographic isolation declines as ranges become progressively subdivided (Chapter 2). While these results certainly should not be interpreted as evidence that intrinsic biology and adaptive mechanisms are unimportant in diversification, they do suggest that geographical processes could also provide a general explanation for variation in species diversity across clades.

6.1.2 The limits to the geographic ranges of species

In Chapter 3, I showed that at large spatial scales, the limits to geographic ranges of bird species are strongly shaped by environmental gradients. At a global scale, 60% of the spatial variation in the shapes of species' ranges was explicable by the effects of temperature, precipitation and the geometric constraints of the continents (Chapter 3). These results support the conventional wisdom, and the countless studies using

environmental niche modelling, that ranges are limited by the spatial variation in the conditions to which a species is adapted (Colwell & Rangel 2009; Grinnell 1914; Guisan & Zimmermann 2000; Hutchinson 1957; Kirkpatrick & Barton 1997; Pulliam 2000).

The simulations used to model range shape were extremely simple, and assumed that geographic ranges were assembled purely by a process of dispersal from a single point in space. This model may reasonably characterise the process of range evolution for species that have arisen recently as small peripheral isolates (Chapter 2). However, if range sizes evolve randomly through time (Chapter 4) then, for older species, the current geographic range is just as likely to have been achieved through a process of range contraction as expansion. Furthermore a model of expansion will be a poor representation for species which have arisen by vicariance, where the geographic range is inherited from the parent (Chapter 2). Incorporating more realistic range dynamics into these models is likely to lead to a greater explanatory power, particularly where species have recently experienced large-scale fluctuations in the extent and position of their range.

Individually based neutral models assume that species' distributions are governed solely by the random death and dispersal of individuals across the landscape (Hubbell 2001). Neutral models thus predict that geographic ranges should be approximately circular in shape and only the effects of the continental boundaries would cause large departures from this (Skellam 1951). Chapter 3 shows that random processes acting at the individual level cannot predict the shapes of species' ranges. While the birth and death of an individual may be governed by a strong element of chance (Hubbell & Foster 1986), the deterministic processes regulating population abundance across species' ranges appear to overwhelm these individual level stochastic events. Over ecological timescales,

therefore, I predict that environmental determinism, not neutrality, will explain species' range limits.

6.1.3 The evolution of geographic ranges

In Chapter 4, I examined the evidence from reconstructed phylogenies that geographic range sizes undergo predictable trajectories over the course of a species' lifetime. I found that the relationship between range size and evolutionary age across birds and mammals did not differ from that expected if range sizes have evolved at random through time. That the patterns in species' range sizes are consistent with random models raises the possibility that stochastic processes play a significant role in range evolution. A greater role for stochasticity does not require accepting that species' distributions are truly random and detached from ecological or environmental causes (Hubbell 2006). Over ecological timescales, geographic ranges are clearly shaped by deterministic processes (Chapter 3). However, when viewed over longer timescales changes in range extent may be dependent on more probabilistic events (Raup et al. 1973), such as the removal or appearance of geological barriers (Weir et al. 2009), long distance dispersal (Carlquist 1981), the appearance of new mutations conferring resistance to pathogens (Ricklefs 2010), the introduction or extinction of natural enemies and the evolution of climatic tolerance (Wiens & Donoghue 2004).

Failing to reject a null model is of course not the same as showing that range evolution occurs at random and there may be deterministic models that are also consistent with the observed patterns. For instance, species' ranges have repeatedly fluctuated in

response to the regular waxing and waning of ice ages (Davies et al. 2009; Dynesius & Jansson 2000), but the signal of this may be indistinguishable from a random walk. I intend to conduct further research to test whether deterministic models are likely to leave a signature in phylogenies.

6.1.4 The effects of ranges on speciation

The reciprocal dynamics between ranges and speciation highlighted in Chapters 2 and 4 may confound standard comparative approaches that attempt to infer the effects of a trait, in this case range size or shape, on rates of diversification. Typically the average value of a trait is compared between sister clades or similarly aged taxonomic groups of differing richness (Barraclough et al. 1995; Cardillo et al. 2003; Isaac et al. 2005; Owens et al. 1999; Stuart-Fox & Owens 2003). A positive correlation would suggest that the trait promotes speciation while a negative correlation would suggest that the trait inhibits speciation. However, because speciation results in the subdivision of ranges, a negative relationship between richness and range size is expected regardless of the direction of the effect of range size on speciation rate. The relationship between range size and species richness therefore provides little information on the effects of species' ranges on diversification.

One way of dealing with the interdependence of ranges and speciation is to examine the effects of geographic ranges on the processes leading to speciation rather than trying to piece together the events after they have happened. In Chapter 5, I tested whether differences in the shapes of geographic ranges resulted in differences in genetic

cohesion across species (Gavrilets et al. 2000; Gavrilets & Losos 2009; Rousset 1997; Wright 1943). I found that range shape was unrelated to levels of gene flow amongst populations and that this was instead predicted by aspects of ecology, including dispersal mode and body size. I argued that because the configuration of geographic ranges is strongly determined by continuously changing climatic gradients (Chapter 3), range shape may be too ephemeral a property to lead to differences in genetic cohesion across species (Futuyma 1987). In this instance, ecology seems to be a more important factor than geographic ranges in explaining the potential for speciation.

Although speciation in the absence of spatial isolation may be rare amongst the terrestrial vertebrates examined in this thesis, in other groups it may form a more important component of diversification, such as ploidy in plants (Grant 1981; Le Comber & Smith 2004). These other modes of speciation may, however, have similar consequences for the dynamics of diversification. For instance, just as the chances of geographic isolation increase with range size, the chances of forming a new polyploid are likely to be a positive function of population size (Rosenzweig 1995). Furthermore, like in the peripatric model, the newly formed species will be much rarer than the parent. These conditions should lead to variation in the rates of speciation and extinction amongst lineages and through time. The general findings of the thesis may therefore be relevant to other groups, where non-geographical models of speciation are more important.

6.2 Geography and the role of ecology in species diversification

In this thesis I have largely discussed geographical and ecological niche related factors as distinct explanations for variation in species diversity. If species' distributions are only weakly related to biological traits or the presence of other species, then treating geography and ecology independently may be justified. However, if ecological differences or interactions amongst species underlie variation in range sizes then the ultimate cause for patterns in diversity would be ecological, with geography merely providing the proximate mechanism. Do the results of this thesis provide any insights into this question?

In Chapter 2, I showed that there is little phylogenetic signal in range size within bird genera. In other words, closely related species often have equally disparate range sizes as more distantly related species. This finding is consistent with previous studies showing that range size exhibits a low phylogenetic signal, with the majority of the variation amongst species occurring at low taxonomic levels (Freckleton et al. 2002; Freckleton & Jetz 2009; Gaston & Blackburn 1997; Jones et al. 2005; Ricklefs 2010; Waldron 2007). Because the ecology and life history of species tend to be much more phylogenetically conserved than range size (Freckleton et al. 2002) this implies that such intrinsic traits have a relatively weak effect on the extent of species' distributions (Ricklefs 2010). Instead, differences in range size may be largely dependent on the effects of past speciation events (Chapter 2), the stochastic processes of range expansion and contraction (Chapter 4) and the properties of the environment in which a species happens to occur (Chapter 3). Studies are now required to test the relative explanatory

power of ecological traits, environmental and historical factors in explaining current variation in range size (Bohning-Gaese et al. 2006; Duncan et al. 1999; Ricklefs & Latham 1992).

In Chapter 3, I showed that range limits in birds are associated with broad scale variation in the climate. A major question left unanswered, however, is whether this association is direct, such as through physiological mechanisms (Kellermann et al. 2009; Root 1988a) or indirect through ecological interactions, such as competition (MacArthur 1972; Price & Kirkpatrick 2009; Terborgh 1985; Terborgh & Weske 1975). The role of competition could be examined in these models by including the presence or absence of species as an additional environmental variable controlling range expansion. However, the potential for competition is likely to be dependent on evolution history, in that only those species occurring in the same place (i.e. not separated by barriers) have the potential to compete, while the strength of competition between species is expected to decline with the time since they diverged (Barraclough & Vogler 2000; Kraft et al. 2007; Letcher et al. 1994). A more tractable approach may therefore be to use the models developed in Chapter 2, to examine the patterns of overlap in geographic ranges expected under varying degrees of competition. From this, it may be possible to quantify the strength of competition occurring amongst species in real clades

If geography does act independently of ecology then what are the implications of this for testing the role of ecology in diversification? If geographic models simply shifted the expected patterns, then testing whether trees departed from this new null model would be a relatively simple procedure. Unfortunately, this is not the case. Instead, when the effects of geography are included, the variety of possible phylogenetic patterns increases

enormously (Chapter 2). As a result, without knowing the geographical context under which a clade has diversified, the patterns expected in the absence of ecological differences become unclear. For instance, a pattern of imbalance may not require additional ecological explanations if speciation had occurred predominantly via peripatry but would if most speciation has occurred by vicariance (Chapter 2). Taken together, this suggests that excluding the role of geography may have serious implications for the study of diversification. Not only may ecological processes be invoked where none are needed, but other patterns which do require additional biological explanations may be overlooked.

6.3 Geography and the role of chance in species diversification

Random processes have largely been rejected as explanations for the variation in species diversity amongst groups (Dial & Marzluff 1989; Heard 1992; Mooers 1995; Slowinski & Guyer 1989; Slowinski & Guyer 1993). However, given that geographic barriers are required to initiate speciation, the explanations for why some lineages speciate while others do not, must involve a strong element of chance, or simply being at the right place at the right time (Anderson & Evensen 1978). Although ecological factors may modulate the effectiveness of barriers (Burney & Brumfield 2009; Kisel & Barraclough 2010) this is a second order effect. Equally, the chances of a species going extinct may be largely dependent, simply on the persistence of the environmental conditions to which it is adapted (Grinnell 1924). The risk of extinction will therefore to a certain extent be independent of species' ecologies.

The chances of encountering a barrier or of dwindling to extinction are likely to be heavily weighted by the size of the geographic range (Rosenzweig 1995; Chapter 2). But in so far as range size is a product of stochastic events (Chapter 4), this only pushes the role of chance deeper into the process of diversification. During geographic isolation one daughter lineage is likely to inherit a larger range than the other (Anderson & Evensen 1978; Waldron 2007; Chapter 2). Because at this point, the incipient species are likely to be ecologically similar, the differing fortunes dealt to species at the outset of their lives will to a large degree be independent of ecology. Those unlucky lineages which inherit smaller geographic ranges have poor prospects for diversification.

While we might be willing to accept that this inherent randomness in speciation could explain why species A rather than species B gave rise to species C, D and E (Gould 1990), the idea that these kinds of events could explain the large scale differences in diversity between clades appears implausible (Dial & Marzluff 1989; Guyer & Slowinski 1993; Heard 1992; Mooers 1995; Mooers & Heard 1997; Slowinski & Guyer 1989; Slowinski & Guyer 1993). However, this may simply be because of biases in our perceptions of the scale at which chance operates (Gould 1985). Clearly we cannot explain the diversity amongst groups by treating every individual speciation and extinction event as a separate toss of the coin (Raup et al. 1973). If instead, stochasticity takes the form of the expansion of a species across a continent (e.g.Ricklefs 2003) or the uplift of a mountain range then these single events may initiate a process of diversification that continues for tens of millions of years. The process of species diversification is therefore no longer a coin tossing exercise, requiring heavily weighted odds, but instead becomes a jackpot lottery where big payoffs can arise from a single

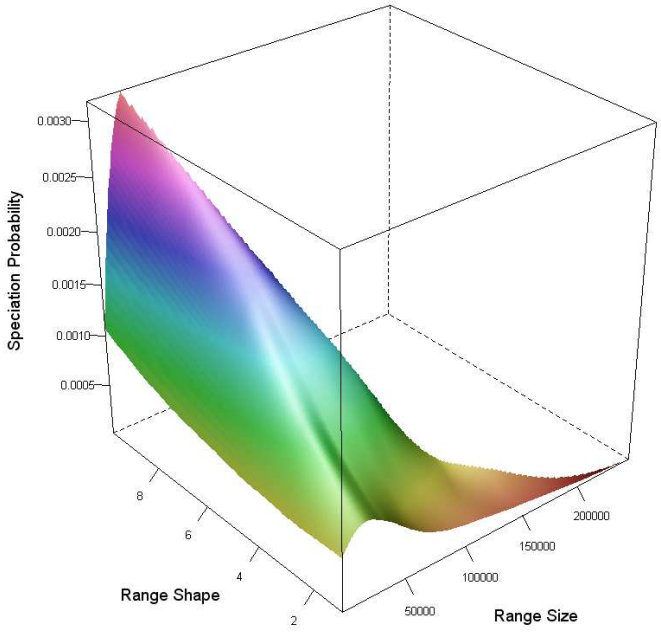
stroke of luck. Under this geographical framework, chance may have a significant role in generating the observed variation in species diversity.

6.4 Conclusions

In this thesis I examined the role of geographic ranges in the evolution of species diversity. Using a combination of phylogenetic and geographic approaches on both simulated and real data I have shown that geographic ranges can have a profound effect on the patterns of diversification. Variation in species diversity usually attributed to ecological processes may instead be the result of the interactions between speciation and the dynamics of geographic ranges. Furthermore, although geographic ranges are limited by deterministic processes, the evolution of species' ranges appears largely stochastic. These results suggest that geography and neutral processes may play a much larger role in the evolution of species diversity than is commonly recognised.

Appendix 1

a)



b)

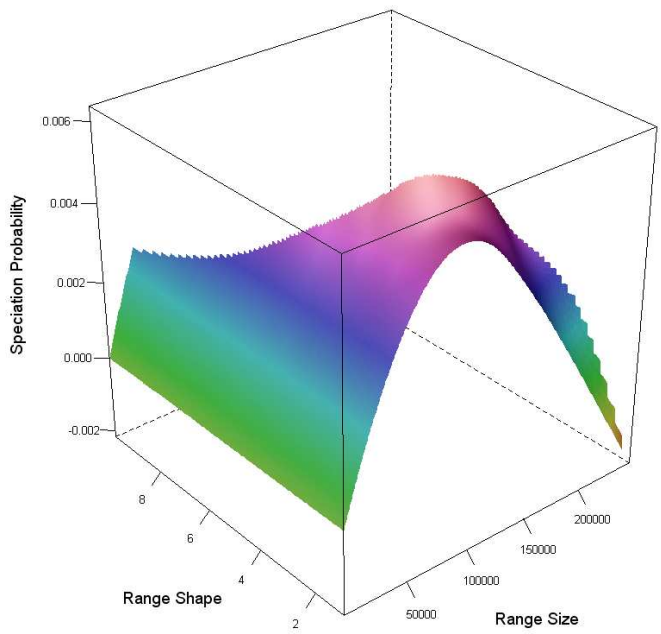


Figure S1. The relationship between range size (units^2), range shape and the probability of speciation under the a) vicariance model under an exponential distribution of barriers lengths (mean length=110 spatial units) and b) peripatric model where the probability of producing a colonist is linearly related to the range area as a proportion of the domain area. Smooth surfaces were fitted using a loess model with a span of 0.4. Range shape is measured as the relative length of the range long and short axis, with higher values indicating more elongated ranges. Length to width ratios greater than 10 are not plotted because given the geometric constraints imposed by the domain boundaries most parameter space would be empty.

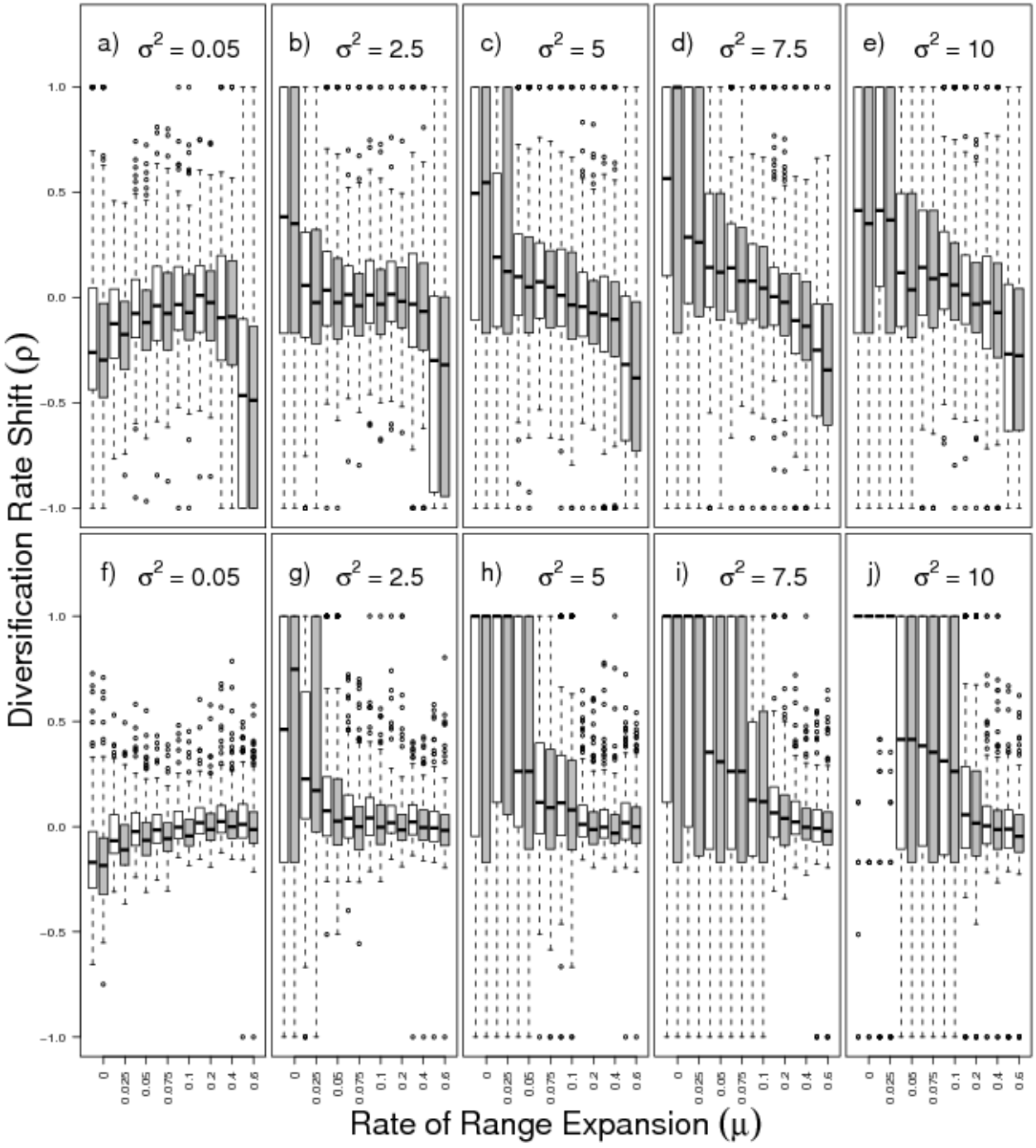


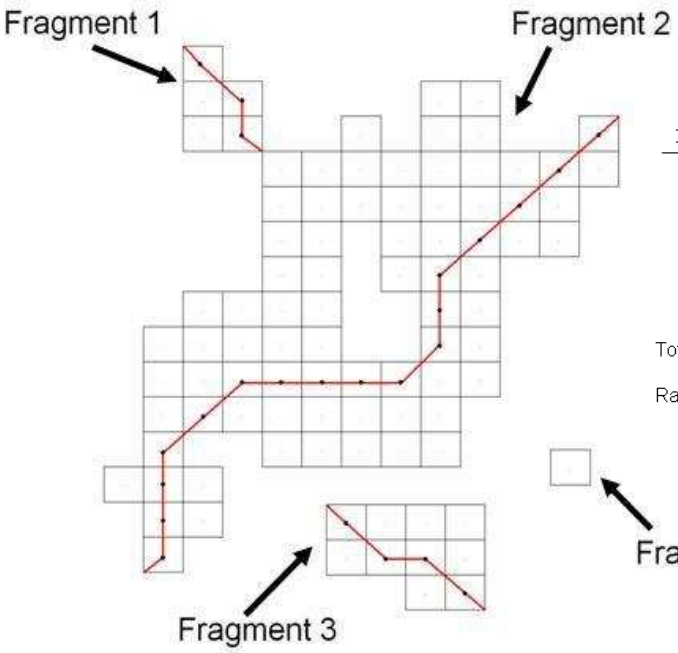
Figure S2. Diversification rate shifts (ρ) for the full range of range expansion (μ) (0, 0.025, 0.05, 0.75, 0.1, 0.2, 0.4, 0.6) and movement variability (σ^2 = 0.05, 2.5, 5, 7.5, 10) parameters explored with a small initial starting range of 150x150 units (9% of the domain) and under the two speciation scenarios a-e) vicariance model, f-j) peripatric model. Results are shown for the complete trees (white boxes) and for when 20% of the extant tips were pruned (grey boxes).

Appendix 2

Range linearity index

To quantify the shape of the total gridded species' range, I first calculated the shape of each of the constituent range fragments (McGarigal & Marks 1995) using graph theory, implemented in the "graph" and "RBGL" packages in R (http://cran.r-project.org/). Fragments were identified as clusters of occupied cells connected by cell edges; cells connected only by their vertices were assumed to be separate fragments (Figure S1). To calculate the longest axis for each fragment, I used the shortest path distance through the range (i.e. passing through adjacent occupied cell centres) (McRae & Beier 2007) between all cells lying on the convex hull of the shape, and selected the longest of these (Figure S2). This measure is preferable to a simple Euclidian distance (Graves 1988), because it accounts for concavity in range fragments (McRae & Beier 2007). In calculating the path length, the distances between adjacent cell centres were measured using great circle distances in the R package "fields" (http://cran.r-project.org/) (cells sharing edges or vertices were treated as adjacent). The use of great circle distances allowed the true distance over the Earths surface between cells to be calculated and so the measure of the range long axis was robust to the distortion of shape that occurs when the globe is viewed on the equal-area Behrman projection. In addition, a constant was added to the path length representing the distance from final cell centres to the actual external cell vertices. The overall range shape for a species was calculated as the average shape across fragments, weighted by fragment area (McGarigal & Marks 1995) (Figure S2).

Fragments smaller than 3 cells have a constant shape and were therefore not included in the calculation of range shape.



Fragment	Size	Long Axis	Range Linearity Index (R_s)
1	5	3.83	$3.83^2 / 5 = 2.93$
2	77	20.31	$20.31^2 / 77 = 5.36$
3	10	5.24	$5.24^2 / 10 = 2.75$
4	1	NA	NA

Total Range Size = 5 +77 + 10
= 92

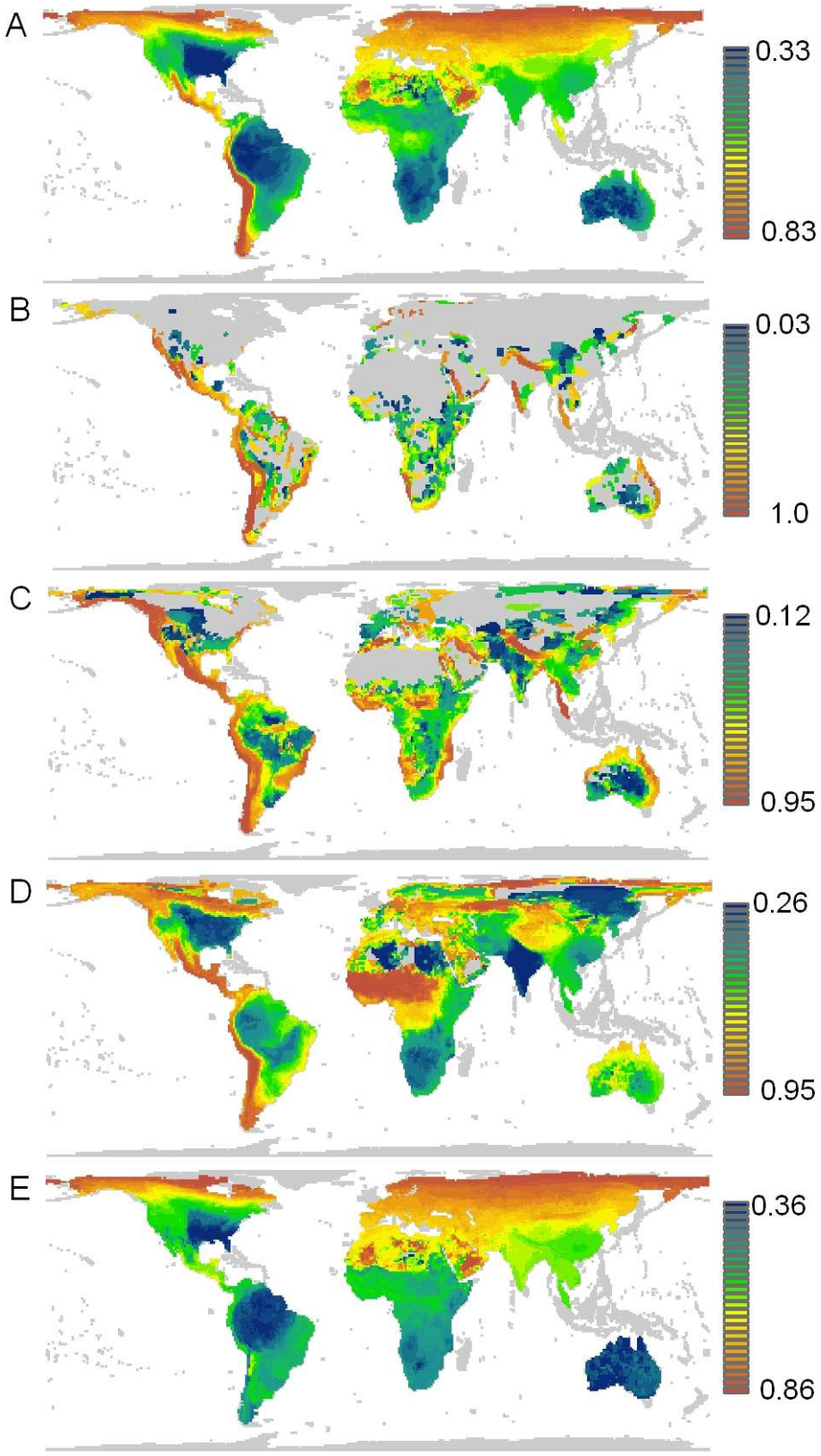
Range Linearity Index = (2.93 x 5/92) + (5.36 x 77/92) + (2.75 x 10/92)
= 4.95

Figure S1. Measuring species' geographic range shape under the area weighted Range Linearity Index for a fictitious species' range. The gridded shape represents the cells occupied by the species within the continental domain. The range consists of 4 fragments or clusters of cells that are disconnected from other clusters. Groups of cells that share only vertices (e.g. Fragment 1 and 2) are treated as separate fragments. Fragment 4 is smaller than 3 cells and so is not included in the measurement of shape. The shape of each fragment is calculated separately. For each fragment, the red line is the shortest path, passing through the centre of adjacent occupied cells, between the two cells furthest apart on the fragment edge. For a given fragment, the shortest path between cells may take a number of routes, but the choice of these is arbitrary.

Maurer's shape index

I calculated an alternative measure of range shape based on the scaled difference in the length of the eigen values of the variance-covariance matrix of distances between occupied cells (Maurer 1994). For full details of the general methodology I refer the reader to Maurer (1994). Here I briefly outline the details of how I applied this method to my global study. I first calculated the mean latitude and longitude of each range fragment and then calculated the great circle distance along the meridians and parallels from each occupied cell centre to these latitudinal and longitudinal averages. I then extracted the eigen values (e_1 and e_2) from the variance-covariance matrix of these internal range distances. Finally, the index of shape (Rs_2) was calculated as the scaled difference between the length of the eigen values according to the following formula; $Rs_2 = (e_1 - e_2)/(e_1 + e_2)$.

Figure S2. On the following page. Spatial patterns in Maurer's Shape Index for observed species' ranges (a) all species and for each range size quartile (b-e) (first, second, third, fourth). Areas in red indicate more elongated distributions, while areas in blue indicate more circular ranges and are plotted in quantiles with 25 levels. Grey cells indicate land area not included in study. Maps are plotted in an equal-area Behrman projection.


A
0.33
0.83
B
0.03
1.0
C
0.12
0.95
D
0.26
0.95
E
0.36
0.86

Predictor	Range Linearity Index				Maurer's Index			
	OLS			UL	OLS			UL
	Intercept	Slope	r^2	r^2	Intercept	Slope	r^2	r^2
Null	0.79	0.79	0.16	0.01	0.49	0.38	0.28	0.03
NPP	1.25	0.27	0.13	0.03	0.47	0.32	0.06	0.01
Precipitation	1.01	0.49	0.15	0.03	0.49	0.27	0.03	0.01
Temperature	0.99	0.47	0.23	0.07	0.45	0.44	0.46	0.06
Elevation	1.02	0.45	0.25	0.07	0.42	0.41	0.14	0.04
TemperatureX Precipitation	0.35	0.90	0.59	0.25	0.22	0.70	0.52	0.37

Table S1. Comparison of global models based on the Range Linearity and Maurer's Shape Index.

Predictor	1st quartile				2nd quartile			
	Int	Slope	r^2	$r^{2\ b}$	Int	Slope	r^2	$r^{2\ b}$
Null	0.63	0.01	0.00	0.00	0.62	-0.01	0.00	0.00
NPP	0.34	0.52	0.11	0.16	0.38	0.42	0.14	0.11
Precipitation	0.32	0.61	0.14	0.17	0.41	0.40	0.12	0.09
Temperature	0.58	0.17	0.01	0.01	0.61	0.02	0.00	0.00
Elevation	0.32	0.58	0.17	0.21	0.40	0.40	0.13	0.10
TemperatureX Precipitation	0.29	0.64	0.19	0.22	0.37	0.48	0.16	0.11

Predictor	3rd quartile				4th quartile			
	Int	Slope	r^2	$r^{2\ b}$	Int	Slope	r^2	$r^{2\ b}$
Null	0.56	0.15	0.05	0.01	0.44	0.48	0.35	0.05
NPP	0.37	0.51	0.26	0.11	0.46	0.30	0.03	0.01
Precipitation	0.37	0.49	0.16	0.08	0.43	0.38	0.02	0.01
Temperature	0.54	0.18	0.07	0.01	0.40	0.52	0.52	0.10
Elevation	0.47	0.28	0.08	0.04	0.38	0.49	0.10	0.03
TemperatureX Precipitation	0.41	0.40	0.15	0.08	0.13	0.83	0.63	0.55

Table S2. Model results for each range size quartile using Maurer's shape Index. Shown are the results from the non-spatial Ordinary Least squares and Unity Line regressions for each range size quartile. Int = Intercept, r^2 is from the OLS regression and $r^{2\ b}$ is from the unity line regressions.

Predictor	Afrotropics				Australasia				Indomalaysia			
	Int	Slope	r^2	$r^{2\ b}$	Int	Slope	r^2	$r^{2\ b}$	Int	Slope	r^2	$r^{2\ b}$
Null	0.30	1.53	0.24	0.01	0.37	0.42	0.05	0.00	0.52	0.26	0.32	0.00
NPP	0.18	0.82	0.37	0.08	0.27	0.50	0.42	0.15	0.50	0.15	0.40	0.01
Precipitation	0.32	0.52	0.23	0.04	0.10	0.82	0.70	0.64	0.49	0.18	0.44	0.01
Temperature	0.44	0.55	0.17	0.00	0.42	0.25	0.05	0.00	0.50	0.28	0.51	0.00
Elevation	0.72	-0.51	0.12	0.01	0.32	0.43	0.02	0.00	0.45	0.26	0.61	0.03
TemperatureX Precipitation	0.35	0.42	0.24	0.05	-0.08	1.10	0.41	0.30	0.49	0.16	0.28	0.03

Predictor	Nearctic				Neotropics				Palearctic			
	Int	Slope	r^2	$r^{2\ b}$	Int	Slope	r^2	$r^{2\ b}$	Int	Slope	r^2	$r^{2\ b}$
Null	0.24	0.71	0.37	0.22	0.34	1.19	0.41	0.03	0.55	0.37	0.35	0.01
NPP	0.62	-0.03	0.00	0.00	0.25	0.63	0.75	0.43	1.05	-0.85	0.15	0.01
Precipitation	0.51	0.24	0.01	0.00	0.20	0.84	0.65	0.28	1.05	-0.89	0.23	0.01
Temperature	0.20	0.75	0.70	0.51	0.24	1.25	0.71	0.09	0.53	0.36	0.50	0.03
Elevation	0.53	0.14	0.01	0.01	0.26	0.63	0.85	0.44	0.70	-0.04	0.00	0.00
TemperatureX Precipitation	0.20	0.73	0.23	0.19	0.20	0.77	0.79	0.46	0.45	0.36	0.08	0.04

Table S3. Model results for each biogeographic realm using Maurer's shape Index.

Shown are the results from the non-spatial Ordinary Least squares and Unity Line regressions for each biogeographic realm (excluding Oceania and Antarctica). Simulations were run on the global domain with species free to expand into adjacent realms if they were connected by land cells. The cells belonging to each realm were then analysed separately. Int = Intercept, r^2 is from the OLS regression and $r^{2\ b}$ is from the unity line regressions.

Appendix 3

Table S1 Range evolution models (REM's) selected for each genus and order across birds and mammals.

Order	Genus	Species richness	REM	slope coefficient	polynomial slope coefficient
Anseriformes	Anas	44	2	+	Na
Anseriformes	Anser	10	1	0	Na
Anseriformes	Aythya	9	1	0	Na
Anseriformes	Cygnus	6	3	-	Na
Anseriformes	Oxyura	7	1	0	Na
Anseriformes	Tadorna	7	1	0	Na
		116	6	+	-
Ciconiiformes	Tringa	15	2	+	Na
Craciformes	Crax	7	3	-	Na
Craciformes	Mitu	7	1	0	Na
		23	7	-	-
Gruiformes	Grus	13	1	0	Na
		15	1	0	Na
Musophagiformes	Tauraco	22	2	+	Na
Passeriformes	Acanthiza	12	2	+	Na
Passeriformes	Amytornis	8	2	+	Na
Passeriformes	Basileuterus	21	6	+	-
Passeriformes	Catharus	12	5	-	+
Passeriformes	Cinclodes	12	1	0	Na
Passeriformes	Dendroica	29	1	0	Na
Passeriformes	Empidonax	15	1	0	Na
Passeriformes	Ficedula	25	1	0	Na
Passeriformes	Geositta	11	1	0	Na
Passeriformes	Geothlypis	10	1	0	Na
Passeriformes	Hemispingus	10	6	+	-
Passeriformes	Hirundo	35	1	0	Na
Passeriformes	Muscisaxicola	12	4	+	+
Passeriformes	Myioborus	12	5	-	+
Passeriformes	Progne	6	6	+	-
Passeriformes	Tachycineta	8	5	-	+
Passeriformes	Tangara	45	1	0	Na
Passeriformes	Thamnophilus	25	1	0	Na
Passeriformes	Turdus	63	1	0	Na
Passeriformes	Vermivora	9	1	0	Na
		424	6	+	-
Piciformes	Pteroglossus	12	6	+	-
Piciformes	Ramphastos	11	4	+	+
		24	1	0	Na

Psittaciformes	Amazona	29	1	0	Na
Trogoniformes	Trogon	17	1	0	Na
		28	1	0	Na
Artiodactyla	Bos	6	7	-	-
Artiodactyla	Capra	8	2	+	Na
Artiodactyla	Cephalophus	14	7	-	-
Artiodactyla	Gazella	7	1	0	Na
Artiodactyla	Martes	7	1	0	Na
Artiodactyla	Mustela	15	1	0	Na
Artiodactyla	Tragelaphus	9	1	0	Na
		83	1	0	Na
Carnivora	Genetta	13	1	0	Na
		57	4	+	+
Chiroptera	Artibeus	18	1	0	Na
Chiroptera	Platyrrhinus	8	1	0	Na
Chiroptera	Sturnira	11	1	0	Na
Chiroptera	Vampyressa	6	2	+	Na
		62	1	0	Na
Dasyuromorphia	Antechinus	8	3	-	Na
Dasyuromorphia	Dasyurus	6	2	+	Na
Dasyuromorphia	Pseudantechinus	6	1	0	Na
Dasyuromorphia	Sminthopsis	18	1	0	Na
		61	1	0	Na
Lagomorpha	Ochotona	27	1	0	Na
Primates	Alouatta	9	2	+	Na
Primates	Hylobates	7	1	0	Na
Primates	Macaca	20	4	+	+
		43	5	-	+
Rodentia	Calomys	10	1	0	Na
Rodentia	Chaetodipus	16	2	+	Na
Rodentia	Dipodomys	19	1	0	Na
Rodentia	Eothenomys	7	1	0	Na
Rodentia	Marmota	14	2	+	Na
Rodentia	Microtus	51	2	+	Na
Rodentia	Perognathus	9	1	0	Na
Rodentia	Spermophilus	38	1	0	Na
Rodentia	Tamias	25	4	+	+
		218	2	+	Na
Soricomorpha	Talpa	8	1	0	Na
		24	2	+	Na

Models were fitted using standard linear and polynomial regressions with the best model selected as the model with the lowest AIC. The species richness of orders may be greater than that of the constituent genera because models were not fit to genera with less that 6 species.

Appendix 4

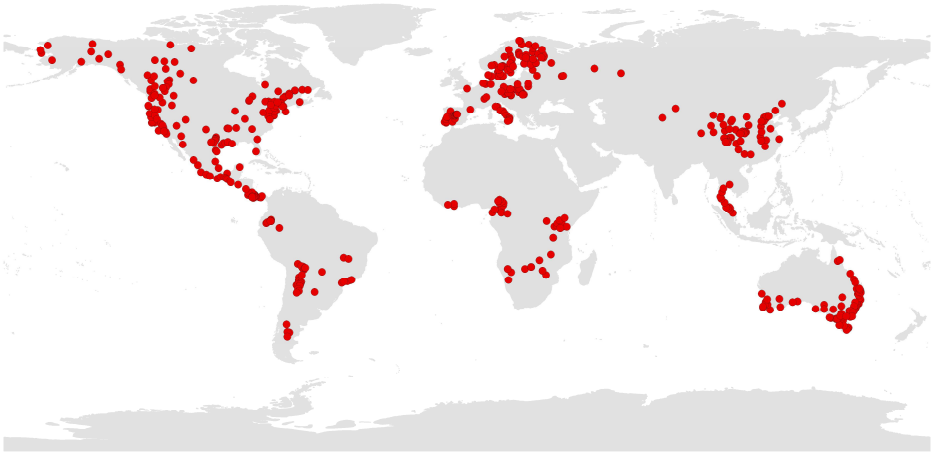


Figure S1. Geographical locations of 554 populations from across the 60 species in the analysis.

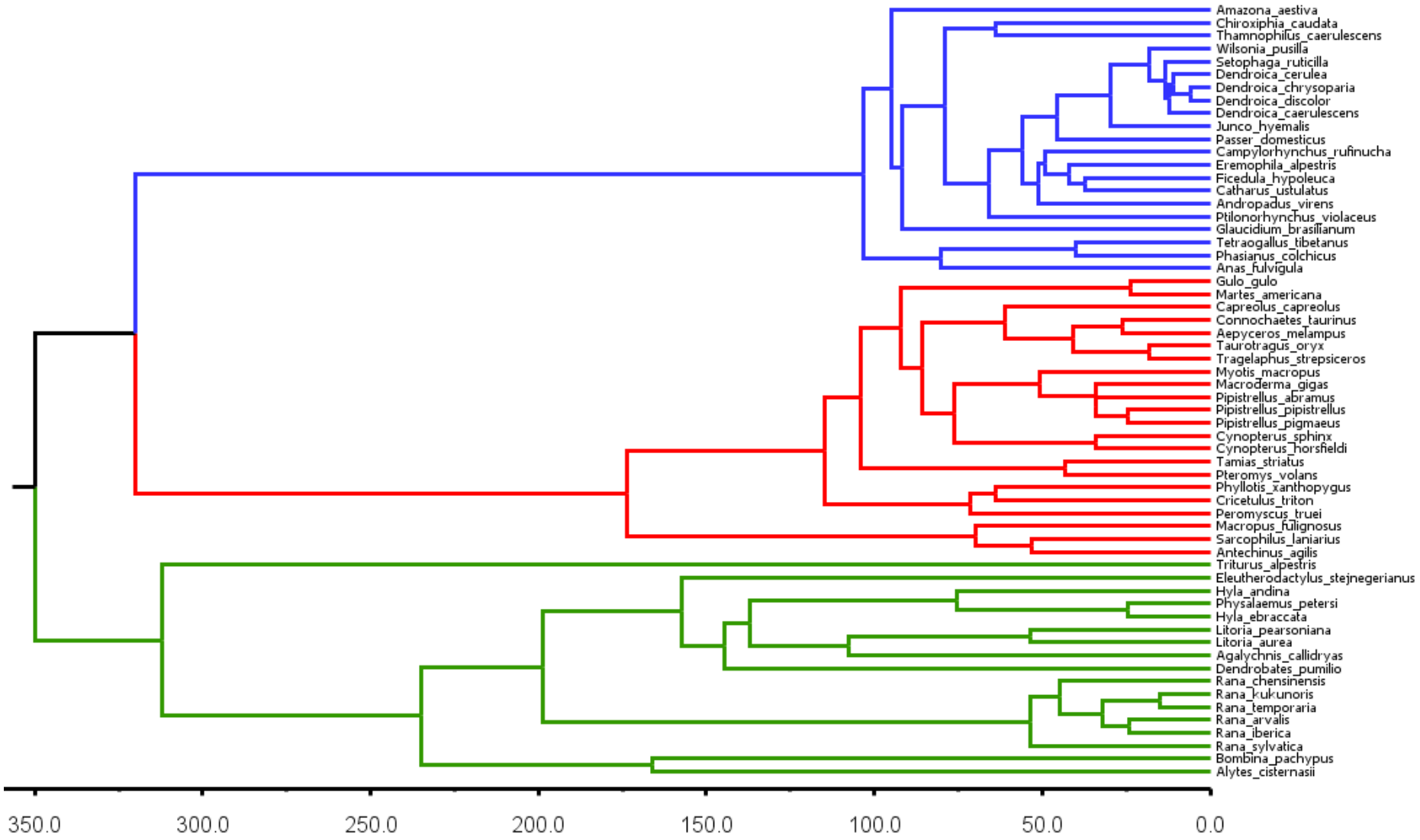


Figure S2. Phylogeny for species of birds (blue), mammals (red) and amphibians (green) included in the analysis. Time scale is in My.

Table S1 Species analysed in this study and references for F_{ST} and body size data.

Species	F_{ST} reference	Body Size reference
Aepyceros melampus	(Lorenzen et al. 2006)	(Jones et al. 2009)
Agalychnis callidryas	(Robertson et al. 2009)	AmphibiaWeb*
Alytes cisternasii	(Goncalves et al. 2009)	AmphibiaWeb*
Amazona aestiva	(Leite et al. 2008)	(Olson et al. 2009)
Anas fulvigula	(McCracken et al. 2001)	(Olson et al. 2009)
Andropadus virens	(Smith et al. 2005)	(Olson et al. 2009)
Antechinus agilis	(Beckman et al. 2007)	(Kraaijeveld-Smit et al. 2002)
Bombina pachypus	(Canestrelli et al. 2006)	(Vukov et al. 2006)
Campylorhynchus rufinucha	(Vazquez-Miranda et al. 2009)	(Olson et al. 2009)
Capreolus capreolus	(Thulin 2006)	(Jones et al. 2009)
Catharus ustulatus	(Ruegg et al. 2006)	(Olson et al. 2009)
Chiroxiphia caudata	(Francisco et al. 2007)	(Olson et al. 2009)
Connochaetes taurinus	(Arctander et al. 1999)	(Jones et al. 2009)
Cricetulus triton	(Xie & Zhang 2005)	(Yongqing et al. 2002)
Cynopterus horsfieldi	(Campbell et al. 2006)	(Funakoshi & Akbar 1997)
Cynopterus sphinx	(Campbell et al. 2006)	(Jones et al. 2009)
Dendrobates pumilio	(Wang & Summers 2010)	AmphibiaWeb*
Dendroica caerulescens	(Davis et al. 2006)	(Olson et al. 2009)
Dendroica cerulea	(Veit et al. 2005)	(Olson et al. 2009)
Dendroica chrysoparia	(Lindsay et al. 2008)	(Olson et al. 2009)
Dendroica discolor	(Buerkle 1999)	(Olson et al. 2009)
Eleutherodactylus stejnegerianus	(Crawford 2003)	(Savage 2002)
Eremophila alpestris	(Drovetski et al. 2005)	(Olson et al. 2009)
Ficedula hypoleuca	(Lehtonen 2009)	(Olson et al. 2009)
Glaucidium brasilianum	(Proudfoot 2005)	(Olson et al. 2009)
Gulo gulo	(Kyle & Strobeck 2001)	(Jones et al. 2009)
Hyla andina	(Koscinski et al. 2009)	(Koscinski et al. 2009)
Hyla ebraccata	(Robertson et al. 2009)	(Wollerman 1999)
Junco hyemalis	(Rasner et al. 2004)	(Olson et al. 2009)
Litoria aurea	(Burns et al. 2004)	(Hamer et al. 2003)
Litoria pearsoniana	(McGuigan et al. 1998)	(McDonald & Davies 1990)
Macroderma gigas	(Wilmer et al. 1999)	(Jones et al. 2009)
Macropus fuliginosus	(Neaves et al. 2009)	(Jones et al. 2009)
Martes americana	(Kyle & Strobeck 2003)	(Jones et al. 2009)
Myotis macropus	(Campbell et al. 2009)	(Jackson 2003)
Passer domesticus	(Kekkonen et al. 2011)	(Olson et al. 2009)
Peromyscus truei	(Turner & Hoekstra 2008)	(Hollander & Vander Wall 2004)
Phasianus colchicus	(Qu et al. 2009)	(Olson et al. 2009)
Phyllotis xanthopygus	(Kim et al. 1998)	(Jones et al. 2009)
Physalaemus petersi	(Funk et al. 2009)	(Boul & Ryan 2004)
Pipistrellus abramus	(Wei et al. 2010)	(Jones et al. 2009)
Pipistrellus pigmaeus	(Bryja et al. 2009)	(Greenaway & Hudson 1990)
Pipistrelluspipistrellus	(Bryja et al. 2009)	(Jones et al. 2009)
Pteromysvolans	(Selonen et al. 2005)	(Jones et al. 2009)
Ptilonorhynchus violaceus	(Nicholls et al. 2006)	(Olson et al. 2009)
Rana arvalis	(Knopp & Merila 2009)	(Knopp 2008)

Rana chensinensis	(Zhan et al. 2009)	(Lu et al. 2006)
Rana iberica	(Martinez-Solano et al. 2005)	AmphibiaWeb*
Rana kukunoris	(Zhao et al. 2009)	(Fei et al. 2009)
Rana sylvatica	(Lee-Yaw et al. 2009)	(Guttman et al. 1995)
Rana temporaria	(Palo et al. 2004)	(Lesbarreres et al. 2007)
Sarcophilus laniarius	(Jones et al. 2004)	(Jones & Barmuta 2000)
Setophaga ruticilla	(Colbeck et al. 2008)	(Olson et al. 2009)
Tamias striatus	(Chambers & Garant 2010)	HAGR+
Taurotragus oryx	(Lorenzen et al. 2010)	(Jones et al. 2009)
Tetraogallus tibetanus	(An et al. 2009)	(Olson et al. 2009)
Thamnophilus caerulescens	(Brumfield 2005)	(Olson et al. 2009)
Tragelaphus strepsiceros	(Nersting & Arctander 2001)	(Jones et al. 2009)
Triturus alpestris	(Pabijan & Babik 2006)	(Denoel et al. 2007)
Wilsonia pusilla	(Clegg et al. 2003)	(Olson et al. 2009)

* http://amphibiaweb.org/

+ Human Ageing Genomic Resources http://genomics.senescence.info/

Sources of F_{ST} and body size data

An, B., Zhang, L. X., Browne, S., Liu, N. F., Ruan, L. Z. & Song, S. 2009 Phylogeography of Tibetan snowcock (Tetraogallus tibetanus) in Qinghai-Tibetan Plateau. *Molecular Phylogenetics and Evolution* **50**, 526-533.

Arctander, P., Johansen, C. & Coutellec-Vreto, M. A. 1999 Phylogeography of three closely related African bovids (tribe Alcelaphini). *Molecular Biology and Evolution* **16**, 1724-1739.

Beckman, J., Banks, S. C., Sunnucks, P., Lill, A. & Taylor, A. C. 2007 Phylogeography and environmental correlates of a cap on reproduction: teat number in a small marsupial, Antechinus agilis. *Molecular Ecology* **16**, 1069-1083.

Boul, K. E. & Ryan, M. J. 2004 Population variation of complex advertisement calls in *Physalaemus petersi* and comparative laryngeal morphology. *Copeia* **3**, 624-631.

Brumfield, R. T. 2005 Mitochondrial variation in Bolivian populations of the variable antshrike (Thamnophilus caerulescens). *Auk* **122**, 414-432.

Bryja, J., Kanuch, P., Fornuskova, A., Bartonicka, T. & Rehak, Z. 2009 Low population genetic structuring of two cryptic bat species suggests their migratory behaviour in continental Europe. *Biological Journal of the Linnean Society* **96**, 103-114.

Buerkle, C. A. 1999 The historical pattern of gene flow among migratory and nonmigratory populations of prairie warblers (Aves : parulinae). *Evolution* **53**, 1915-1924.

Burns, E. L., Eldridge, M. D. B. & Houlden, B. A. 2004 Microsatellite variation and population structure in a declining Australian Hylid Litoria aurea. *Molecular Ecology* **13**, 1745-1757.

Campbell, P., Schneider, C. J., Adnan, A. M., Zubaid, A. & Kunz, T. H. 2006 Comparative population structure of Cynopterus fruit bats in peninsular Malaysia and southern Thailand. *Molecular Ecology* **15**, 29-47.

Campbell, S., Guay, P. J., Mitrovski, P. J. & Mulder, R. 2009 Genetic differentiation among populations of a specialist fishing bat suggests lack of suitable habitat connectivity. *Biological Conservation* **142**, 2657-2664.

Canestrelli, D., Cimmaruta, R., Costantini, V. & Nascetti, G. 2006 Genetic diversity and phylogeography of the Apennine yellow-bellied toad Bombina pachypus, with implications for conservation. *Molecular Ecology* **15**, 3741-3754.

Chambers, J. L. & Garant, D. 2010 Determinants of Population Genetic Structure in Eastern Chipmunks (Tamias striatus): The Role of Landscape Barriers and Sex-Biased Dispersal. *Journal of Heredity* **101**, 413-422.

Clegg, S. M., Kelly, J. F., Kimura, M. & Smith, T. B. 2003 Combining genetic markers and stable isotopes to reveal population connectivity and migration patterns in a Neotropical migrant, Wilson's warbler (Wilsonia pusilla). *Molecular Ecology* **12**, 819-830.

Colbeck, G. J., Gibbs, H. L., Marra, P. P., Hobson, K. & Webster, M. S. 2008 Phylogeography of a widespread North American migratory songbird (Setophaga ruticilla). *Journal of Heredity* **99**, 453-463.

Crawford, A. J. 2003 Huge populations and old species of Costa Rican and Panamanian dirt frogs inferred from mitochondrial and nuclear gene sequences. *Molecular Ecology* **12**, 2525-2540.

Davis, L. A., Roalson, E. H., Cornell, K. L., McClanahan, K. D. & Webster, M. S. 2006 Genetic divergence and migration patterns in a North American passerine bird: implications for evolution and conservation. *Molecular Ecology* **15**, 2141-2152.

Denoel, M., Lena, J. & Joly, P. 2007 Morph switching in a dimorphic population of *Triturus alpestris* (Amphibia, Caudata). *Evolutionary Ecology* **21**, 325-335.

Drovetski, S. V., Pearson, S. F. & Rohwer, S. 2005 Streaked horned lark Eremophila alpestris strigata has distinct mitochondrial DNA. *Conservation Genetics* **6**, 875-883.

Fei , L., Hu, S., Ye, C. & Huang, Y. 2009 *Fauna Sinica, Amphibia*. Fauna Sinica Amphibia. Beijing: Science Press.

Francisco, M. R., Gibbs, H. L., Galetti, M., Lunardi, V. O. & Galetti, P. M. 2007 Genetic structure in a tropical lek-breeding bird, the blue manakin (Chiroxiphia caudata) in the Brazilian Atlantic Forest. *Molecular Ecology* **16**, 4908-4918.

Funakoshi, K. & Akbar, Z. 1997 Behavioural and reproductive ecology of the dog-faced fruit bats, *Cynopterus brachyotis* and *C. horsfeldi*, in a Malaysian rainforest. *Mammal Study* **22**, 95-108.

Funk, W. C., Cannatella, D. C. & Ryan, M. J. 2009 Genetic divergence is more tightly related to call variation than landscape features in the Amazonian frogs Physalaemus petersi and P-freibergi. *Journal of Evolutionary Biology* **22**, 1839-1853.

Goncalves, H., Martinez-Solano, I., Pereira, R. J., Carvalho, B., Garcia-Paris, M. & Ferrand, N. 2009 High levels of population subdivision in a morphologically conserved Mediterranean toad (Alytes cisternasii) result from recent, multiple refugia: evidence from mtDNA, microsatellites and nuclear genealogies. *Molecular Ecology* **18**, 5143-5160.

Greenaway, F. & Hudson, A. M. 1990 *A field guide to British bats*. Uxbridge: Bruce Coleman Books.

Guttman, D., Bramble, J. E. & Sexton, O. J. 1995 Observations on the breeding immigration of wood frogs *Rana sylvatica* reintroduced in East-central Missouri. *American Midland Naturalist* **125**, 269-274.

Hamer, A. J., Lane, S. J. & Mahoney, M. J. 2003 Retreat site selection during winter in the green and golden bell frog *Litoria aurea* Lesson. *Journal of Herpetology* **7**, 541-545.

Hollander, J. L. & Vander Wall, S. B. 2004 Effectiveness of six species of rodents as dispersers of singleleaf pinon pine (*Pinus monophylla*). *Oecologia* **138**, 57-65.

Jackson , S. 2003 *Australian mammals: biology and captive management* Collingwood: CSIRO.

Jones, K. E., Bielby, J. & Cardillo, M. 2009 PanTHERIA: a species-level database of life history, ecology, and geography of extant and recently extinct mammals. *Ecology* **90**.

Jones, M. E. & Barmuta, L. A. 2000 Niche differentiation among sympatric Australian dasyurid carnivores *Journal of Mammalogy* **81**, 434-447.

Jones, M. E., Paetkau, D., Geffen, E. & Moritz, C. 2004 Genetic diversity and population structure of Tasmanian devils, the largest marsupial carnivore. *Molecular Ecology* **13**, 2197-2209.

Kekkonen, J., Seppa, P., Hanski, I. K., Jensen, H., Vaisanen, R. A. & Brommer, J. E. 2011 Low genetic differentiation in a sedentary bird: house sparrow population genetics in a contiguous landscape. *Heredity* **106**, 183-190.

Kim, I., Phillips, C. J., Monjeau, J. A., Birney, E. C., Noack, K., Pumo, D. E., Sikes, R. S. & Dole, J. A. 1998 Habitat islands, genetic diversity, and gene flow in a Patagonian rodent. *Molecular Ecology* **7**, 667-678.

Knopp, T. 2008 Phylogeography and population genetic of the moor frog (*Rana arvalis* Nilsson) in northern Europe. In *Department of Biological and Environmental Sciences*, vol. Doctor of Philosophy: Helsinki.

Knopp, T. & Merila, J. 2009 Microsatellite variation and population structure of the moor frog (Rana arvalis) in Scandinavia. *Molecular Ecology* **18**, 2996-3005.

Koscinski, D., Yates, A. G., Handford, P. & Lougheed, S. C. 2009 Effects of landscape and history on diversification of a montane, stream-breeding amphibian. *Journal of Biogeography* **36**, 255-265.

Kraaijeveld-Smit, F. J. L., Ward, S. J., Temple-Smith, P. D. & Paetkau, D. 2002 Factors influencing paternity success in Antechinus agilis: last-male sperm precedence, timing of mating and genetic compatibility *Journal of Evolutionary Biology* **15**, 100-107.

Kyle, C. J. & Strobeck, C. 2001 Genetic structure of North American wolverine (Gulo gulo) populations. *Molecular Ecology* **10**, 337-347.

Kyle, C. J. & Strobeck, C. 2003 Genetic homogeneity of Canadian mainland marten populations underscores the distinctiveness of Newfoundland pine martens (Martes americana atrata). *Canadian Journal of Zoology-Revue Canadienne De Zoologie* **81**, 57-66.

Lee-Yaw, J. A., Davidson, A., Mcrae, B. H. & Green, D. M. 2009 Do landscape processes predict phylogeographic patterns in the wood frog? *Molecular Ecology* **18**, 1863-1874.

Lehtonen, P. K. 2009 Geographic patterns of genetic differentiation and plumage colour variation are different in the pied flycatcher (Ficedula hypoleuca). *Molecular Ecology* **18**, 4463-4476.

Leite, K. C. E., Seixas, G. H. F., Berkunsky, I., Collevatti, R. G. & Caparroz, R. 2008 Population genetic structure of the blue-fronted Amazon (Amazona aestiva, Psittacidae: Aves) based on nuclear microsatellite loci: implications for conservation. *Genetics and Molecular Research* **7**, 819-829.

Lesbarreres, D., Schmeller, D. S., Primmer, C. R. & Merila, J. 2007 Genetic variability predicts common frog (Rana temporaria) size at metamorphosis in the wild. *Heredity* **99**, 41-46.

Lindsay, D. L., Barr, K. R., Lance, R. F., Tweddale, S. A., Hayden, T. J. & Leberg, P. L. 2008 Habitat fragmentation and genetic diversity of an endangered, migratory songbird, the golden-cheeked warbler (Dendroica chrysoparia). *Molecular Ecology* **17**, 2122-2133.

Lorenzen, E. D., Arctander, P. & Siegismund, H. R. 2006 Regional genetic structuring and evolutionary history of the impala Aepyceros melampus. *Journal of Heredity* **97**, 119-132.

Lorenzen, E. D., Masembe, C., Arctander, P. & Siegismund, H. R. 2010 A long-standing Pleistocene refugium in southern Africa and a mosaic of refugia in East Africa: insights from mtDNA and the common eland antelope. *Journal of Biogeography* **37**, 571-581.

Lu, X., Li, B. & Liang, J. J. 2006 Comparative demography of a temperate anuran, *Rana chensinensis*, along a relatively fine elevational gradient. *Canadian Journal of Zoology* **84**, 1789-1795.

Martinez-Solano, I., Rey, I. & Garcia-Paris, M. 2005 The impact of historical and recent factors on genetic variability in a mountain frog: the case of Rana iberica (Anura : Ranidae). *Animal Conservation* **8**, 431-441.

McCracken, K. G., Johnson, W. P. & Sheldon, F. H. 2001 Molecular population genetics, phylogeography, and conservation biology of the mottled duck. *Conservation Genetics* **2**, 87-102.

McDonald, K. R. & Davies, M. 1990 Morphology and biology of the Australian tree frog *Litoria pearsoniana* (Copland)(Anura: Hylidae). *Transactions of the Royal Society of South Australia* **114**, 145-156.

McGuigan, K., McDonald, K., Parris, K. & Moritz, C. 1998 Mitochondrial DNA diversity and historical biogeography of a wet forest-restricted frog (Litoria pearsoniana) from mid-east Australia. *Molecular Ecology* **7**, 175-186.

Neaves, L. E., Zenger, K. R., Prince, R. I. T., Eldridge, M. D. B. & Cooper, D. W. 2009 Landscape discontinuities influence gene flow and genetic structure in a large, vagile Australian mammal, Macropus fuliginosus. *Molecular Ecology* **18**, 3363-3378.

Nersting, L. G. & Arctander, P. 2001 Phylogeography and conservation of impala and greater kudu. *Molecular Ecology* **10**, 711-719.

Nicholls, J. A., Austin, J. J., Moritz, C. & Goldizen, A. W. 2006 Genetic population structure and call variation in a passerine bird, the satin bowerbird, Ptilonorhynchus violaceus. *Evolution* **60**, 1279-1290.

Olson, V. A., Davies, R. G., Orme, C. D. L., Thomas, G. H., Meiri, S., Blackburn, T. M., Gaston, K. J., Owens, I. P. F. & Bennett, P. M. 2009 Global biogeography and ecology of body size in birds. *Ecology Letters* **12**, 249-259.

Pabijan, M. & Babik, W. 2006 Genetic structure in northeastern populations of the Alpine newt (Triturus alpestris): evidence for post-Pleistocene differentiation. *Molecular Ecology* **15**, 2397-2407.

Palo, J. U., Schmeller, D. S., Laurila, A., Primmer, C. R., Kuzmin, S. L. & Merila, J. 2004 High degree of population subdivision in a widespread amphibian. *Molecular Ecology* **13**, 2631-2644.

Proudfoot, G. A. 2005 Mitochondrial and nucelar assessment of Ferruginous Pygmy-owl (Glaucidum brasilianum) phylogeography vol. Doctor of Philosophy: Texas A&M University.

Qu, J. Y., Liu, N. F., Bao, X. K. & Wang, X. L. 2009 Phylogeography of the ring-necked pheasant (Phasianus colchicus) in China. *Molecular Phylogenetics and Evolution* **52**, 125-132.

Rasner, C. A., Yeh, P., Eggert, L. S., Hunt, K. E., Woodruff, D. S. & Price, T. D. 2004 Genetic and morphological evolution following a founder event in the dark-eyed junco, Junco hyemalis thurberi. *Molecular Ecology* **13**, 671-681.

Robertson, J. M., Duryea, M. C. & Zamudio, K. R. 2009 Discordant patterns of evolutionary differentiation in two Neotropical treefrogs. *Molecular Ecology* **18**, 1375-1395.

Ruegg, K., Slabbekoorn, H., Clegg, S. & Smith, T. B. 2006 Divergence in mating signals correlates with ecological variation in the migratory songbird, Swainson's thrush (Catharus ustulatus). *Molecular Ecology* **15**, 3147-3156.

Savage, J. M. 2002 *The amphibians and reptiles of Costa Rica: a hepetofauna between two continents, between two seas*. Chicago: University of Chicago Press.

Selonen, V., Painter, J. N. & Hanski, I. K. 2005 Microsatellite variation in the Siberian flying squirrel in Finland. *Annales Zoologici Fennici* **42**, 505-511.

Smith, T. B., Calsbeek, R., Wayne, R. K., Holder, K. H., Pires, D. & Bardeleben, C. 2005 Testing alternative mechanisms of evolutionary divergence in an African rain forest passerine bird. *Journal of Evolutionary Biology* **18**, 257-268.

Thulin, C. G. 2006 Microsatellite investigation of roe deer (Capreolus capreolus) in Scandinavia reveals genetic differentiation of a Baltic Sea Island population. *European Journal of Wildlife Research* **52**, 228-235.

Turner, L. M. & Hoekstra, H. E. 2008 Reproductive protein evolution within and between species: maintenance of divergent ZP3 alleles in Peromyscus. *Molecular Ecology* **17**, 2616-2628.

Vazquez-Miranda, H., Navarro-Siguenza, A. G. & Omland, K. E. 2009 Phylogeography of the Rufous-Naped Wren (Campylorhynchus Rufinucha): Speciation and Hybridization in Mesoamerica. *Auk* **126**, 765-778.

Veit, M. L., Robertson, R. J., Hamel, P. B. & Friesen, V. L. 2005 Population genetic structure and dispersal across a fragmented landscape in cerulean warblers (Dendroica cerulea). *Conservation Genetics* **6**, 159-174.

Vukov, T. D., Dzukic, G., Lelo, S., Borkin, L. J., Litvinchuk, S. N. & Kalezic, M. L. 2006 Morphometrics of the yellow-bellied toad (*Bombina variegata*) in the

central balkans: Implications for taxonomy and zoogeography. *Zoological Studies* **45**.
Wang, I. J. & Summers, K. 2010 Genetic structure is correlated with phenotypic divergence rather than geographic isolation in the highly polymorphic strawberry poison-dart frog. *Molecular Ecology* **19**, 447-458.
Wei, L., Flanders, J. R., Rossiter, S. J., Miller-Butterworth, C. M., Zhang, L. B. & Zhang, S. Y. Y. 2010 Phylogeography of the Japanese pipistrelle bat, Pipistrellus abramus, in China: the impact of ancient and recent events on population genetic structure. *Biological Journal of the Linnean Society* **99**, 582-594.
Wilmer, J. W., Hall, L., Barratt, E. & Moritz, C. 1999 Genetic structure and male-mediated gene flow in the ghost bat (Macroderma gigas). *Evolution* **53**, 1582-1591.
Wollerman, L. 1999 Acoustic interference limits call detection in a Neotropical frog *Hyla ebraccata*. *Animal Behaviour* **57**, 529-536.
Xie, J. Y. & Zhang, Z. B. 2005 Mitochondrial DNA phylogeography of populations of Cricetulus triton in the North China Plain. *Journal of Mammalogy* **86**, 833-840.
Yongqing, W., Zhibin, Z. & Laixian, X. 2002 The genetic diversity of central and peripheral populations of ratlike hamster (*Cricetulus triton*). *Chinese Science Bulletin* **47**, 201-206.
Zhan, A. B., Li, C. & Fu, J. Z. 2009 Big mountains but small barriers: Population genetic structure of the Chinese wood frog (Rana chensinensis) in the Tsinling and Daba Mountain region of northern China. *Bmc Genetics* **10**, -.
Zhao, S., Dai, Q. & Fu, J. 2009 Do rivers function as genetic barriers for the plateau wood frog at high elevations? *Journal of Zoology* **279**, 270-276.

Table S2 Genbank accession numbers for species included in the phylogenetic tree.

Species	Rag1	Cytb	ND2	Coi
Aepyceros melampus		*AF034966*		
Agalychnis annae	*EF174311*	*GQ365913*		
Agalychnis callidryas	*AY323765*			
Agalychnis moreletii	*EF174314*	*GQ365916*		
Agalychnis saltator	*EF174315*	*GQ365917*		
Alauda arvensis	*AY056978*	*AF074595*	*DQ125975*	*GQ481297*
Alytes cisternasii		*AY442019*		
Alytes obstetricans	*AY583334*	*AY514027*		
Amazona aestiva				*FJ027053*
Amazona farinose	*DQ143346*	*AY283475*	*AY194461*	*AY194394*
Amazona xanthops	*DQ143345*	*AY669441*	*AY669485*	*AY301465*
Amazonetta brasiliensis	*AF427042*	*AF059054*		*FJ027059*
Anas fulvigula		*AF059074*	*AF059134*	*DQ432723*
Andropadus virens	*AY443265*	*EU619756*	*AY049527*	
Antechinus agilis		*DQ842137*		
Antechinus stuartii	*AY125023*	*AF038285*		
Bombina pachypus		*DQ320148*		*EU531200*
Bombina variegate		*EF212676*		*DQ138375*
Bos Taurus	*AF447520*	*AY521030*		
Boulengerula boulengeri	*EF107322*	*EU200987*		
Campylorhynchus fasciatus	*AY228007*	*DQ004883*		
Campylorhynchus rufinucha		*DQ004888*	*AY460230*	
Capreolus capreolus		*Y14951*		
Catharus ustulatus	*AY443265*	*EU619756*	*AY049527*	*DQ434531*
Chiroxiphia caudata	*FJ501612*	*AF453819*	*AY136620*	*FJ027349*
Chlorocichla flaviventris	*AY228009*	*AY228053*	*GQ242087*	
Connochaetes taurinus		*AF016638*		
Craugastor tabasarae		*DQ350248*		*FJ766682*
Craugastor talamancae		*EF629457*		*EF629430*
Cricetulus migratorius	*AY294956*	*AY288508*		
Cricetulus triton		*AJ973388*		
Cynopterus horsfieldi		*EF201643*		
Cynopterus sphinx	*AF203758*	*DQ445703*		
Dendrobates arboreus		*DQ502467*		*DQ502763*
Dendrobates pumilio	*EU325918*	*EU934599*		*DQ502909*
Dendrobates vicentei		*DQ502602*		*DQ502869*
Dendroica caerulescens		*EU815674*	*AY650188*	*DQ434561*
Dendroica cerulea		*EU815676*	*AY650193*	*DQ432885*
Dendroica chrysoparia			*EU815773*	
Dendroica discolor		*EU815678*	*AY650214*	*AY666458*
Eleutherodactylus coqui	*EF107341*	*EF636954*		
Eleutherodactylus stejnegerianus				*EF562411*
Engystomops pustulosus	*EF107299*	*GU086762*		*FJ766700*
Eremophila alpestris		*AF290137*	*AF407049*	*GQ481853*
Ficedula hypoleuca	*AY228018*	*AJ299683*	*DQ146345*	*GQ481897*

Gallus gallus	*NM_001031188*	*EU839454*		*FJ808635*
Geothlypis aequinoctialis	*AY228019*	*FJ653048*	*FJ605320*	*FJ027622*
Glaucidium bolivianum	*EU348894*	*AJ003975*		
Glaucidium brasilianum		*AJ003976*	*AF039672*	*FJ027628*
Glaucomys volans	*AY241472*	*AF157921*		
Gulo gulo	*AB109340.1*	*X94921*		
Hyla andina		*AY549371*		
Hyla ebraccata		*AY843853*		
Hyla intermedia	*FJ227095*	*FJ226881*		*FJ226787*
Hyla meridionalis	*FJ227085*	*FJ226896*		*FJ226807*
Hyla orientalis	*FJ227062*	*FJ226855*		*FJ226831*
Hyla sarda	*FJ227092*	*FJ226905*		*FJ226816*
Hyla savignyi	*FJ227058*	*FJ226912*		*FJ226823*
Ischnocnema guentheri	*GQ345276*	*GQ345196*		
Junco hyemalis		*EU325787*	*AF407044*	*DQ434613*
Litoria aurea	*EF174309*	*AY843937*		*EU043162*
Litoria caerulea	*EF174310*	*AY218782*		*AY883980*
Litoria infrafrenata		*AY843940*		*FJ952337*
Litoria pearsoniana				
Macroderma gigas	*AY834654*			
Macropus fuliginosus	*FJ603234.1*	*AY099271*		
Macropus rufogriseus	*FJ603240*	*EF368026*		
Macropus rufus	*FJ607154*	*U87136*		
Martes americana	*DQ660270*	*AB051234*		
Myotis macropus		*AJ841959*		
Myotis velifer	*AY249868*	*AF376870*		
Odocoileus virginianus	*EU189399*	*DQ379370*		
Parula pitiayumi	*AY228025*	*AY216822*	*AF256500*	*EU815664*
Passer domesticus	*EF568263*	*AY495393*	*EF449664*	*DQ434705*
Passerella iliaca	*EF568271*	*AY124544*	*AY138933*	*DQ433874*
Peromyscus leucopus	*EF369771*	*EF989980*		
Peromyscus maniculatus	*EF369744*	*EF666239*		
Peromyscus truei		*FJ800579*		
Petaurista petaurista	*AY241473*			
Phasianus colchicus		*AF028798*	*AF222561*	*GQ482362*
Phyllastrephus zosterops	*AY319996*		*AF199391*	
Phyllotis bonariensis	*AY963252*	*AY956731*		
Phyllotis limatus	*AY963236*	*AY956740*		
Phyllotis xanthopygus	*AY241466*	*AF108693*		
Physalaemus cuvieri		*AY843975*		
Physalaemus petersi				*DQ120042*
Pipistrellus abramus		*AB085739*		
Pipistrellus pigmaeus		*DQ120855*		
Pipistrellus pipistrellus		*AJ504443*		
Pteromysvolans		*AB164478*		
Ptilonorhynchus violaceus	*AY057026*	*X74256*	*AY064759*	
Pycnonotus sinensis	*EU447155*	*EU447109*	*GU112672*	*FJ661088*
Rana arvalis		*AY522383*		

Rana chensinensis		*AF077396*		
Rana iberica		*AY147965*		
Rana kukunoris	*GQ285780*			
Rana sylvatica	*DQ019511*	*AY083271*		*EF525849*
Rana temporaria	*AY323776*	*AY522428*		
Sarcophilus laniarius	*EF551556*			
Setophaga ruticilla		*AF383008*	*AF383124*	*DQ434741*
Tamias striatus	*AY011879*	*AY292715*		
Taurotragus oryx		*AF036278*		
Tetraogallus tibetanus		*EU839456*	*EU845746*	
Thamnophilus caerulescens	*FJ461176*	*EF030325*	*EF030294*	*FJ028405*
Tragelaphus strepsiceros		*AF036280*		
Triturus alpestris		*DQ821209*		*EF525923*
Triturus marmoratus	*AY583354*	*DQ821253*		*EF526008*
Wilsonia pusilla		*AY216865*	*AY650220*	*DQ434828*

Species highlighted in gray are those with F_{ST} data and that were included in the analysis. Sequence data for species not highlighted were included to help resolve the tree but were subsequently pruned. *Litoria pearsoniana* is highlighted in red because sequence data was not available for this species.

Table S3 MAM of the predictors of species F_{ST} with and without phylogeny and at varying spatial scales

Geographic Scale			Non-phylogenetic				Phylogenetic			
	Fixed Terms	Interactions	Posterior mean	1-95% CI	u-95%	P	Posterior mean	1-95% CI	u-95%	P
100km			**0.063**	**0.006**	**0.118**	**0.027**	**0.076**	**0.020**	**0.138**	**0.012**
	Range Shape		0.028	-0.005	0.064	0.105	0.019	-0.012	0.050	0.215
	Marker		**0.883**	**0.667**	**1.127**	**<0.0002**	**0.854**	**0.415**	**1.293**	**<0.0002**
	Latitude		-0.001	-0.002	0.000	0.121	-0.001	-0.002	0.000	0.061
	Dispersal Mode		**0.117**	**0.036**	**0.193**	**0.007**	**0.066**	**0.016**	**0.118**	**0.015**
	Body Mass		**-0.007**	**-0.013**	**-0.001**	**0.016**	-0.007	-0.015	0.000	0.059
		Range Shape x Mitochondria	-0.075	-0.162	0.007	0.075	-0.075	-0.205	0.053	0.252
		Range Shape x Latitude	-0.001	-0.001	0.000	0.160	0.000	-0.001	0.000	0.306
		Range Shape x Body Mass	-0.002	-0.007	0.002	0.292				
		Mitochondria x Latitude	**-0.016**	**-0.021**	**-0.012**	**<0.0002**	**-0.016**	**-0.024**	**-0.006**	**0.000**
		Mitochondria x Non-volant					0.037	-0.271	0.349	0.818
		Mitochondria x Body Mass	**-0.057**	**-0.082**	**-0.032**	**<0.0002**	**-0.054**	**-0.083**	**-0.024**	**<0.0002**
		Latitude x Non-volant	-0.001	-0.003	0.001	0.241				
	DIC = -258.5583						DIC = -249.3573			

Scale	Fixed Terms	Interactions	Posterior mean	1-95% CI	u-95%	P	Posterior mean	1-95% CI	u-95%	P
500km			0.082	-0.008	0.169	0.073	0.094	-0.028	0.235	0.141
	Range Shape						0.006	-0.006	0.018	0.350
	Marker		**1.170**	**0.788**	**1.540**	**<0.0002**	**1.197**	**0.800**	**1.581**	**<0.0002**
	Latitude		**-0.002**	**-0.004**	**0.000**	**0.049**	-0.002	-0.004	0.000	0.068
	Dispersal Mode		**0.221**	**0.095**	**0.344**	**0.001**	**0.194**	**0.029**	**0.361**	**0.027**
	Body Mass		-0.011	-0.030	0.010	0.279	-0.009	-0.035	0.019	0.506
		Range Shape x Mitochondria					-0.058	-0.158	0.044	0.264
		Mitochondria x Latitude	**-0.022**	**-0.029**	**-0.015**	**<0.0002**	**-0.023**	**-0.030**	**-0.015**	**<0.0002**
		Mitochondria x Body Mass	**-0.051**	**-0.082**	**-0.018**	**0.002**	**-0.056**	**-0.091**	**-0.022**	**0.003**
		Latitude x Non-volant	-0.002	-0.004	0.001	0.156	-0.001	-0.004	0.002	0.418
		Latitude x Body Mass	0.000	0.000	0.001	0.106	0.000	0.000	0.001	**0.116**
		Non-volant x Body Mass	**-0.016**	**-0.032**	**-0.002**	**0.035**	**-0.022**	**-0.044**	**0.000**	**0.041**
	DIC = -256.0265						DIC = -244.0842			

Scale	Fixed Terms	Interactions	Posterior mean	1-95% CI	u-95%	P	Posterior mean	1-95% CI	u-95%	P
900km			**0.106**	**0.009**	**0.204**	**0.038**	0.102	-0.024	0.230	0.109
	Range Shape		0.004	-0.006	0.014	0.437				
	Marker		**1.250**	**0.721**	**1.847**	**<0.0002**	**1.210**	**0.775**	**1.616**	**<0.0002**
	Latitude		**-0.002**	**-0.005**	**0.000**	**0.035**	**-0.002**	**-0.005**	**0.000**	**0.038**
	Dispersal Mode		**0.242**	**0.098**	**0.386**	**0.000**	**0.235**	**0.067**	**0.405**	**0.013**
	Body Mass		-0.013	-0.035	0.008	0.228	-0.011	-0.038	0.016	0.411
		Range Shape x Mitochondria	-0.021	-0.200	0.149	0.830				
		Mitochondria x Latitude	**-0.024**	**-0.035**	**-0.014**	**<0.0002**	**-0.023**	**-0.031**	**-0.015**	**<0.0002**
		Mitochondria x Non-volant	0.003	-0.402	0.390	0.994				
		Mitochondria x Body Mass	**-0.050**	**-0.092**	**-0.008**	**0.022**	**-0.044**	**-0.079**	**-0.009**	**0.014**
		Latitude x Non-volant	-0.002	-0.005	0.001	0.221	-0.002	-0.005	0.002	0.313
		Latitude x Body Mass	0.000	0.000	0.001	0.093	0.001	0.000	0.001	0.086
		Non-volant x Body Mass	**-0.020**	**-0.036**	**-0.004**	**0.016**	**-0.024**	**-0.047**	**-0.003**	**0.032**
	DIC = -250.1688						DIC = -245.3584			

Scale	Fixed Terms	Interactions	Posterior mean	1-95% CI	u-95%	P	Posterior mean	1-95% CI	u-95%	P
1300km			**0.117**	**0.014**	**0.215**	**0.024**	0.111	-0.018	0.236	0.080
	Range Shape		0.005	-0.005	0.015	0.370				
	Marker		**1.217**	**0.728**	**1.728**	**<0.0002**	**1.206**	**0.757**	**1.636**	**<0.0002**
	Latitude		**-0.003**	**-0.005**	**-0.001**	**0.022**	**-0.003**	**-0.005**	**0.000**	**0.023**
	Dispersal Mode		**0.271**	**0.103**	**0.415**	**0.001**	**0.264**	**0.086**	**0.441**	**0.005**
	Body Mass		-0.014	-0.036	0.008	0.199	-0.012	-0.039	0.017	0.357
		Range Shape x Mitochondria	-0.007	-0.134	0.131	0.915				
		Mitochondria x Latitude	**-0.024**	**-0.033**	**-0.015**	**<0.0002**	**-0.024**	**-0.032**	**-0.015**	**<0.0002**
		Mitochondria x Body Mass	-0.042	-0.085	0.002	0.064	**-0.040**	**-0.076**	**-0.003**	**0.035**
		Latitude x Non-volant	-0.002	-0.005	0.001	0.232	-0.002	-0.005	0.002	0.298
		Latitude x Body Mass	0.001	0.000	0.001	0.079	0.001	0.000	0.001	0.066
		Non-volant x Body Mass	**-0.022**	**-0.039**	**-0.005**	**0.008**	**-0.026**	**-0.050**	**-0.005**	**0.025**
	DIC = -244.7199						DIC = -240.6001			

Species F_{ST} values were estimated from the OLS regression of F_{ST} against IR at resistance values equivalent to 100, 500, 900 and 1300km. Dispersal mode and Marker are categorical variables with "Volant" and "microsatellite" set as the baseline respectively. Body mass (g) is log-transformed. Significant effects at the 5% level are highlighted in bold.

Bibliography

Abe, F. R. & Lieberman, B. S. 2009 The Nature of Evolutionary Radiations: A Case Study Involving Devonian Trilobites. *Evolutionary Biology* **36**, 225-234.

Agapow, P. M., Bininda-Emonds, O. R. P., Crandall, K. A., Gittleman, J. L., Mace, G. M., Marshall, J. C. & Purvis, A. 2004 The impact of species concept on biodiversity studies. *Quarterly Review of Biology* **79**, 161-179.

Agapow, P. M. & Purvis, A. 2002 Power of eight tree shape statistics to detect nonrandom diversification: A comparison by simulation of two models of cladogenesis. *Systematic Biology* **51**, 866-872.

Aldous, D. J. 1996 Probability distributions on cladograms. In *Random discrete structures. IMA volumes in mathematics and its applications* (ed. D. J. Aldous & R. Permantle), pp. 1-18. Berlin: Springer.

Aleixo, A. 2006 Historical diversification of floodplain forest specialist species in the Amazon: a case study with two species of the avian genus Xiphorhynchus (Aves : Dendrocolaptidae). *Biological Journal of the Linnean Society* **89**, 383-395.

Alexander, R. M. 2002 The merits and implications of travel by swimming, flight and running for animals of different sizes. *Integrative and Comparative Biology* **42**, 1060-1064.

Alfaro, M. E., Santini, F., Brock, C., Alamillo, H., Dornburg, A., Rabosky, D. L., Carnevale, G. & Harmon, L. J. 2009 Nine exceptional radiations plus high turnover explain species diversity in jawed vertebrates. *Proceedings of the National Academy of Sciences of the United States of America* **106**, 13410-13414.

Anderson, C. D., Epperson, B. K., Fortin, M. J., Holderegger, R., James, P. M. A., Rosenberg, M. S., Scribner, K. T. & Spear, S. 2010 Considering spatial and temporal scale in landscape-genetic studies of gene flow. *Molecular Ecology* **19**, 3565-3575.

Anderson, S. 1974 Patterns of faunal evolution. *The Quarterly Review of Biology* **49**, 311-332.

Anderson, S. 1985 The theory of range-size (RS) distributions. *American Museum novitates* **2833**, 1-20.

Anderson, S. & Evensen, M. K. 1978 Randomness in allopatric speciation. *Systematic Zoology* **27**, 421-430.

Antonovics, J. 1976 Nature of limits to natural-selection. *Annals of the Missouri Botanical Garden* **63**, 224-247.

Bahn, V. & McGill, B. J. 2007 Can niche-based distribution models outperform spatial interpolation? *Global Ecology and Biogeography* **16**, 733-742.

Barker, F. K., Cibois, A., Schikler, P., Feinstein, J. & Cracraft, J. 2004 Phylogeny and diversification of the largest avian radiation. *Proceedings of the National Academy of Sciences of the United States of America* **101**, 11040-11045.

Barraclough, T. G., Harvey, P. H. & Nee, S. 1995 Sexual selection and taxonomic diversity in Passerine birds. *Proceedings of the Royal Society B-Biological Sciences* **259**, 211-215.

Barraclough, T. G., Hogan, J. E. & Vogler, A. P. 1999 Testing whether ecological factors promote cladogenesis in a group of tiger beetles (Coleoptera : Cicindelidae).

Proceedings of the Royal Society of London Series B-Biological Sciences **266**, 1061-1067.
Barraclough, T. G. & Nee, S. 2001 Phylogenetics and speciation. *Trends in Ecology & Evolution* **16**, 391-399.
Barraclough, T. G. & Vogler, A. P. 2000 Detecting the geographical pattern of speciation from species-level phylogenies. *American Naturalist* **155**, 419-434.
Beale, C. M., Lennon, J. J. & Gimona, A. 2008 Opening the climate envelope reveals no macroscale associations with climate in European birds. *Proceedings of the National Academy of Sciences of the United States of America* **105**, 14908-14912.
Bell, G. 2001 Neutral macroecology. *Science* **293**, 2413-2418.
Bellemain, E. & Ricklefs, R. E. 2008 Are islands the end of the colonization road? *Trends in Ecology & Evolution* **23**, 461-468.
Belliure, J., Sorci, G., Moller, A. P. & Clobert, J. 2000 Dispersal distances predict subspecies richness in birds. *Journal of Evolutionary Biology* **13**, 480-487.
Bennett, P. M. & Owens, I. P. F. 2002 *Evolutionary Ecology of Birds: Life Histories, Mating Systems and Extinction*. Oxford: Oxford University Press.
Bininda-Emonds, O. R. P., Cardillo, M., Jones, K. E., MacPhee, R. D. E., Beck, R. M. D., Grenyer, R., Price, S. A., Vos, R. A., Gittleman, J. L. & Purvis, A. 2007 The delayed rise of present-day mammals. *Nature* **446**, 507-512.
Blows, M. W. & Hoffmann, A. A. 2005 A reassessment of genetic limits to evolutionary change. *Ecology* **86**, 1371-1384.
Blum, M. G. B. & Francois, O. 2006 Which random processes describe the tree of life? A large-scale study of phylogenetic tree imbalance. *Systematic Biology* **55**, 685-691.
Bohning-Gaese, K., Caprano, T., van Ewijk, K. & Veith, M. 2006 Range size: Disentangling current traits and phylogenetic and biogeographic factors. *American Naturalist* **167**, 555-567.
Bohning-Gaese, K., Gonzalez-Guzman, L. I. & Brown, J. H. 1998 Constraints on dispersal and the evolution of the avifauna of the Northern Hemisphere. *Evolutionary Ecology* **12**, 767-783.
Bohonak, A. J. 1999 Dispersal, gene flow, and population structure. *Quarterly Review of Biology* **74**, 21-45.
Bossart, J. L. & Prowell, D. P. 1998 Genetic estimates of population structure and gene flow: limitations, lessons and new directions. *Trends in Ecology & Evolution* **13**, 202-206.
Brooks, J. L. 1950 Speciation in ancient lakes. *The Quarterly Review of Biology* **25**, 30-60.
Brown, J. H. & Maurer, B. A. 1989 Macroecology - the division of food and space among species on continents. *Science* **243**, 1145-1150.
Brown, J. H., Stevens, G. C. & Kaufman, D. M. 1996 The geographic range: Size, shape, boundaries, and internal structure. *Annual Review of Ecology and Systematics* **27**, 597-623.
Brown, W. L. 1957 Centrifugal speciation. *The Quarterly Review of Biology* **32**, 247-277.
Burney, C. W. & Brumfield, R. T. 2009 Ecology predicts levels of genetic differentiation in Neotropical birds. *American Naturalist* **174**, 358-368.

Cardillo, M., Huxtable, J. S. & Bromham, L. 2003 Geographic range size, life history and rates of diversification in Australian mammals. *Journal of Evolutionary Biology* **16**, 282-288.
Cardillo, M., Orme, C. D. L. & Owens, I. P. F. 2005 Testing for latitudinal bias in diversification rates: An example using New World birds. *Ecology* **86**, 2278-2287.
Carlquist, S. 1981 Chance dispersal *American Scientist* **69** 509-516.
Chan, K. M. A. & Moore, B. R. 1999 Accounting for mode of speciation increases power and realism of tests of phylogenetic asymmetry. *American Naturalist* **153**, 332-346.
Channell, R. & Lomolino, M. V. 2000 Dynamic biogeography and conservation of endangered species. *Nature* **403**, 84-86.
Chown, S. L. 1997 Speciation and rarity: separating cause from consequence. In *The Biology of Rarity. London: Chapman & Hall* (ed. W. E. Kunin & K. J. Gaston), pp 91-109. London Chapman & Hall.
Colwell, R. K. & Lees, D. C. 2000 The mid-domain effect: geometric constraints on the geography of species richness. *Trends in Ecology & Evolution* **15**, 70-76.
Colwell, R. K. & Rangel, T. F. 2009 Hutchinson's duality: The once and future niche. *Proceedings of the National Academy of Sciences of the United States of America* **106**, 19651-19658.
Cooper, N., Bielby, J., Thomas, G. H. & Purvis, A. 2008 Macroecology and extinction risk correlates of frogs. *Global Ecology and Biogeography* **17**, 211-221.
Cornell, H. V. & Lawton, J. H. 1992 Species interactions, local and regional processes, and limits to the richness of ecological communities - a theoretical perspective. *Journal of Animal Ecology* **61**, 1-12.
Coyne, J. A. & Orr, H. A. 2004 *Speciation*. Sunderland: Sinauer Associates.
Coyne, J. A. & Price, T. D. 2000 Little evidence for sympatric speciation in island birds. *Evolution* **54**, 2166-2171.
Cracraft, J. 1982 A nonequilibrium theory for the rate-control of speciation and extinction and the origin of macroevolutionary patterns. *Systematic Zoology* **31**, 348-365.
Currie, D. J., Mittelbach, G. G., Cornell, H. V., Field, R., Guegan, J. F., Hawkins, B. A., Kaufman, D. M., Kerr, J. T., Oberdorff, T., O'Brien, E. & Turner, J. R. G. 2004 Predictions and tests of climate-based hypotheses of broad-scale variation in taxonomic richness. *Ecology Letters* **7**, 1121-1134.
Cushman, S. A. & Landguth, E. L. 2010 Scale dependent inference in landscape genetics. *Landscape Ecology* **25**, 967-979.
Damuth, J. 1981 Population-density and body size in mammals. *Nature* **290**, 699-700.
Darwin, C. 1859 *On the origin of species by means of natural selection or the preservation of favoured races in the struggle for life*. London: John Murray.
Davies, R. G., Orme, C. D. L., Storch, D., Olson, V. A., Thomas, G. H., Ross, S. G., Ding, T. S., Rasmussen, P. C., Bennett, P. M., Owens, I. P. F., Blackburn, T. M. & Gaston, K. J. 2007 Topography, energy and the global distribution of bird species richness. *Proceedings of the Royal Society B-Biological Sciences* **274**, 1189-1197.
Davies, T. J., Barraclough, T. G., Chase, M. W., Soltis, P. S., Soltis, D. E. & Savolainen, V. 2004 Darwin's abominable mystery: Insights from a supertree of the

angiosperms. *Proceedings of the National Academy of Sciences of the United States of America* **101**, 1904-1909.
Davies, T. J., Purvis, A. & Gittleman, J. L. 2009 Quaternary climate change and the geographic ranges of mammals. *American Naturalist* **174**, 297-307.
Davies, T. J., Savolainen, V., Chase, M. W., Goldblatt, P. & Barraclough, T. G. 2005 Environment, area and diversification in the species-rich flowering plant family Iridaceae. *American Naturalist* **166**, 418-425.
Davis, M. B. & Shaw, R. G. 2001 Range shifts and adaptive responses to Quaternary climate change. *Science* **292**, 673-679.
Deichmann, J. L., Duellman, W. E. & Williamson, G. B. 2008 Predicting biomass from snout-vent length in new world frogs. *Journal of Herpetology* **42**, 238-245.
Dial, K. P. & Marzluff, J. M. 1989 Nonrandom diversification within taxonomic assemblages. *Systematic Zoology* **38**, 26-37.
Diamond, J. M. 1973 Distributional ecology of New Guinea birds. *Science* **179**, 759-769.
Dieckmann, U. & Doebeli, M. 1999 On the origin of species by sympatric speciation. *Nature* **400**, 354-357.
Drummond, A. J., Kearse, M., Heled, J. & Moir, R. 2006 Geneious v1.0. Available: http://www.geneious.com/. Accessed November 20th 2010.
Drummond, A. J. & Rambaut, A. 2007 BEAST: Bayesian evolutionary analysis by sampling trees. *Bmc Evolutionary Biology* **7**, 214.
Duncan, R. P., Blackburn, T. M. & Veltman, C. J. 1999 Determinants of geographical range sizes: a test using introduced New Zealand birds. *Journal of Animal Ecology* **68**, 963-975.
Dynesius, M. & Jansson, R. 2000 Evolutionary consequences of changes in species' geographical distributions driven by Milankovitch climate oscillations. *Proceedings of the National Academy of Sciences of the United States of America* **97**, 9115-9120.
Ehrlich, P. R. & Raven, P. H. 1970 Differentiation of populations. *Science* **167**, 1228-1232.
Endler, J. A. 1977 *Geographic variation, speciation and clines*. Monographs in Population Biology. Princeton: Princeton University Press.
Etienne, R. S., Apol, M. E. F., Olff, H. & Weissing, F. J. 2007 Modes of speciation and the neutral theory of biodiversity. *Oikos* **116**, 241-258.
Farrell, B., Dussourd, D. E. & Mitter, C. 1991 Escalation of plant defense: Do latex and resin canals spur plant diversification? *American Naturalist* **138**.
Finlay, B. J. 2002 Global dispersal of free-living microbial eukaryote species. *Science* **296**, 1061-1063.
FitzJohn, R. G., Maddison, W. P. & Otto, S. P. 2009 Estimating trait-dependent speciation and extinction rates from incompletely resolved phylogenies. *Systematic Biology* **58**, 595-611.
Fjeldsa, J. & Rahbek, C. 2006 Diversification of tanagers, a species rich bird group, from lowlands to montane regions of South America. *Integrative and Comparative Biology* **46**, 72-81.
Foote, M., Crampton, J. S., Beu, A. G. & Cooper, R. A. 2008 On the bidirectional relationship between geographic range and taxonomic duration. *Paleobiology* **34**, 421-433.

Foote, M., Crampton, J. S., Beu, A. G., Marshall, B. A., Cooper, R. A., Maxwell, P. A. & Matcham, I. 2007 Rise and fall of species occupancy in Cenozoic fossil mollusks. *Science* **318**, 1131-1134.

Freckleton, R. P. 2000 Phylogenetic tests of ecological and evolutionary hypotheses: checking for phylogenetic independence. *Functional Ecology* **14**, 129-134.

Freckleton, R. P., Harvey, P. H. & Pagel, M. 2002 Phylogenetic analysis and comparative data: A test and review of evidence. *American Naturalist* **160**, 712-726.

Freckleton, R. P. & Jetz, W. 2009 Space versus phylogeny: disentangling phylogenetic and spatial signals in comparative data. *Proceedings of the Royal Society B-Biological Sciences* **276**, 21-30.

Futuyma, D. J. 1987 On the role of species in anagenesis. *American Naturalist* **130**, 465-473.

Gaston, K. J. 1994 Measuring geographic range sizes. *Ecography* **17**, 198-205.

Gaston, K. J. 1998 Species-range size distributions: products of speciation, extinction and transformation. *Philosophical Transactions of the Royal Society of London Series B-Biological Sciences* **353**, 219-230.

Gaston, K. J. 2003 *The structure and dynamics of geographic ranges*. Oxford: Oxford University Press.

Gaston, K. J. 2009 Geographic range limits: achieving synthesis. *Proceedings of the Royal Society B-Biological Sciences* **276**, 1395-1406.

Gaston, K. J. & Blackburn, T. M. 1997 Age, area and avian diversification. *Biological Journal of the Linnean Society* **62**, 239-253.

Gaston, K. J., Davies, R. G., Orme, C. D. L., Olson, V. A., Thomas, G. H., Ding, T. S., Rasmussen, P. C., Lennon, J. J., Bennett, P. M., Owens, I. P. F. & Blackburn, T. M. 2007 Spatial turnover in the global avifauna. *Proceedings of the Royal Society B-Biological Sciences* **274**, 1567-1574.

Gavrilets, S. 2004 *Fitness landscapes and the origin of species* Monographs in Population Biology Princeton: Princeton Uiversity Press.

Gavrilets, S., Li, H. & Vose, M. D. 2000 Patterns of parapatric speciation. *Evolution* **54**, 1126-1134.

Gavrilets, S. & Losos, J. B. 2009 Adaptive radiation: contrasting theory with data. *Science* **323**, 732-737.

Gleason, H. A. 1926 The individualistic concept of the plant association. *Bulletin of the Torrey Botanical Club* **53**, 7-26.

Goldberg, E. E. & Lande, R. 2007 Species' borders and dispersal barriers. *American Naturalist* **170**, 297-304.

Gotelli, N. J., Anderson, M. J., Arita, H. T., Chao, A., Colwell, R. K., Connolly, S. R., Currie, D. J., Dunn, R. R., Graves, G. R., Green, J. L., Grytnes, J. A., Jiang, Y. H., Jetz, W., Lyons, S. K., McCain, C. M., Magurran, A. E., Rahbek, C., Rangel, T. F. L. V. B., Soberon, J., Webb, C. O. & Willig, M. R. 2009 Patterns and causes of species richness: a general simulation model for macroecology. *Ecology Letters* **12**, 873-886.

Gould, S. J. 1985 The paradox of the first tier: An agenda for paleobiology. *Paleobiology* **11**, 2-12.

Gould, S. J. 1990 *Wonderful life: The Burgess Shale and the nature of history*. New York: Norton.

Gould, S. J., Raup, D. M., Sepkoski, J. J., Schopf, T. J. M. & Simberloff, D. S. 1977 The shape of evolution: a comparison or real and random clades. *Paleobiology* **3**, 23-40.

Grant, P. R. & Grant, B. R. 2007 *How and why species multiply: the radiation of Darwin's finches* Princeton: University Press.

Grant, V. 1981 *Plant speciation*. New York: Columbia University Press.

Graves, G. R. 1988 Linearity of geographic range and its possible effect on the population structure of Andean birds. *The Auk* **105**, 47-52.

Graves, G. R. & Rahbek, C. 2005 Source pool geometry and the assembly of continental avifaunas. *Proceedings of the National Academy of Sciences of the United States of America* **102**, 7871-7876.

Greenslade, P. J. M. 1968 Island atterns in the Solomon Islands bird fauna. *Evolution* **22**, 751-761.

Grinnell, J. 1914 Barriers to distribution as regards birds and mammals. *American Naturalist* **48**, 248-245.

Grinnell, J. 1917 Field tests of theories concerning distributional control. *American Naturalist* **51**, 115-128.

Grinnell, J. 1924 Geography and evolution. *Ecology* **5**, 225-229.

Grosholz, E. D. 1996 Contrasting rates of spread for introduced species in terrestrial and marine systems. *Ecology* **77**, 1680-1686.

Guisan, A. & Zimmermann, N. E. 2000 Predictive habitat distribution models in ecology. *Ecological Modelling* **135**, 147-186.

Guyer, C. & Slowinski, J. B. 1993 Adaptive radiation and the topology of large phylogenies. *Evolution* **47**, 253-263.

Hadfield, J. D. & Nakagawa, S. 2010 General quantitative genetic methods for comparative biology: phylogenies, taxonomies and multi-trait models for continuous and categorical characters. *Journal of Evolutionary Biology* **23**, 494-508.

Haffer, J. 1969 Speciation in Amazonian forest birds. *Science* **165** 131-137.

Harmon, L. J., Schulte, J. A., Larson, A. & Losos, J. B. 2003 Tempo and mode of evolutionary radiation in iguanian lizards. *Science* **301**, 961-964.

Harvey, P. H. & Pagel, M. 1991 *The comparative method in evolutionary biology*. Oxford: Oxford University Press.

Hawkins, B. A. & Diniz-Filho, J. A. F. 2006 Beyond Rapoport's rule: Evaluating range size patterns of New World birds in a two-dimensional framework. *Global Ecology and Biogeography* **15**, 461-469.

Hawkins, B. A., Field, R., Cornell, H. V., Currie, D. J., Guegan, J. F., Kaufman, D. M., Kerr, J. T., Mittelbach, G. G., Oberdorff, T., O'Brien, E. M., Porter, E. E. & Turner, J. R. G. 2003 Energy, water, and broad-scale geographic patterns of species richness. *Ecology* **84**, 3105-3117.

Heard, S. B. 1992 Patterns in tree balance among cladistic, phenetic, and randomly generated phylogenetic trees. *Evolution* **46**, 1818-1826.

Heard, S. B. 1996 Patterns in phylogenetic tree balance with variable and evolving speciation rates. *Evolution* **50**, 2141-2148.

Heard, S. B. & Mooers, A. O. 2002 Signatures of random and selective mass extinctions in phylogenetic tree balance. *Systematic Biology* **51**, 889-897.

Hedges, S. B., Parker, P. H., Sibley, C. G. & Kumar, S. 1996 Continental breakup and the ordinal diversification of birds and mammals. *Nature* **381**, 226-229.
Hewitt, G. 2000 The genetic legacy of the Quaternary ice ages. *Nature* **405**, 907-913.
Ho, S. Y. W. & Phillips, M. J. 2009 Accounting for calibration uncertainty in phylogenetic estimation of evolutionary divergence times. *Systematic Biology* **58**, 367-380.
Holt, R. D. 2003 On the evolutionary ecology of species' ranges. *Evolutionary Ecology Research* **5**, 159-178.
Holt, R. D. & Gomulkiewicz, R. 1997 How does immigration influence local adaptation? A reexamination of a familiar paradigm. *American Naturalist* **149**, 563-572.
Holt, R. D., Keitt, T. H., Lewis, M. A., Maurer, B. A. & Taper, M. L. 2005 Theoretical models of species' borders: single species approaches. *Oikos* **108**, 18-27.
Hubbell, S. P. 2001 *The unified neutral theory of biodiversity and biogeography*. Princeton: Princeton University Press.
Hubbell, S. P. 2006 Neutral theory and the evolution of ecological equivalence. *Ecology* **87**, 1387-1398.
Hubbell, S. P. & Foster, R. B. 1986 Biology, chance and history and the structure of tropical rain forest tree communities. In *Community ecology* (ed. J. M. Diamond & T. J. Case), pp. 314-329. New York: Harper and Row
Hughes, C. & Eastwood, R. 2006 Island radiation on a continental scale: Exceptional rates of plant diversification after uplift of the Andes. *Proceedings of the National Academy of Sciences of the United States of America* **103**, 10334-10339.
Huntley, B., Green, R. E., Collingham, Y. C., Hill, J. K., Willis, S. G., Bartlein, P. J., Cramer, W., Hagemeijer, W. J. M. & Thomas, C. J. 2004 The performance of models relating species geographical distributions to climate is independent of trophic level. *Ecology Letters* **7**, 417-426.
Hurlbert, A. H. & Jetz, W. 2007 Species richness, hotspots, and the scale dependence of range maps in ecology and conservation. *Proceedings of the National Academy of Sciences of the United States of America* **104**, 13384-13389.
Hutchinson, G. E. 1957 Concluding remarks. *Cold Spring Harbor Symposium Quantitative Biology* **22**, 415–427.
Hutchinson, G. E. & MacArthur, R. H. 1959 A theoretical ecological model of size distributions among species of animals. *American Naturalist* **93**, 117-125.
Hutchison, D. W. & Templeton, A. R. 1999 Correlation of pairwise genetic and geographic distance measures: Inferring the relative influences of gene flow and drift on the distribution of genetic variability. *Evolution* **53**, 1898-1914.
Imhoff, M. L., Bounoua, L., Ricketts, T., Loucks, C., Harriss, R. & Lawrence, W. T. 2004 Global patterns in human consumption of net primary production. *Nature* **429**, 870-873.
Irwin, D. E., Bensch, S. & Price, T. D. 2001 Speciation in a ring. *Nature* **409**, 333-337.
Isaac, N. J. B., Jones, K. E., Gittleman, J. L. & Purvis, A. 2005 Correlates of species richness in mammals: Body size, life history, and ecology. *American Naturalist* **165**, 600-607.
Jablonski, D. 1987 Heritability at the species level - analysis of geographic ranges of Cretaceous mollusks. *Science* **238**, 360-363.

Jablonski, D. 1995 Extinction in the fossil record. In *Extinction rates* (ed. R. M. May & J. H. Lawton), pp. 25-44. Oxford: Oxford University Press.
Jablonski, D. 2008 Species selection: theory and data. *Annual Review of Ecology Evolution and Systematics* **39**, 501-524.
Jablonski, D. & Hunt, G. 2006 Larval ecology, geographic range, and species survivorship in Cretaceous mollusks: Organismic versus species-level explanations. *American Naturalist* **168**, 556-564.
Jablonski, D. & Roy, K. 2003 Geographical range and speciation in fossil and living molluscs. *Proceedings of the Royal Society B-Biological Sciences* **270**, 401-406.
Jablonski, D., Roy, K. & Valentine, J. W. 2006 Out of the tropics: Evolutionary dynamics of the latitudinal diversity gradient. *Science* **314**, 102-106.
Jansson, R. & Dynesius, M. 2002 The fate of clades in a world of recurrent climatic change: Milankovitch oscillations and evolution. *Annual Review of Ecology and Systematics* **33**, 741-777.
Janz, N., Nylin, S. & Wahlberg, N. 2006 Diversity begets diversity: host expansions and the diversification of plant-feeding insects. *Bmc Evolutionary Biology* **6**, 4.
Janzen, D. H. 1967 Why mountain passes are higher in the tropics. *American Naturalist* **101**, 233-249.
Jenkins, D. G., Brescacin, C. R., Duxbury, C. V., Elliott, J. A., Evans, J. A., Grablow, K. R., Hillegass, M., LyonO, B. N., Metzger, G. A., Olandese, M. L., Pepe, D., Silvers, G. A., Suresch, H. N., Thompson, T. N., Trexler, C. M., Williams, G. E., Williams, N. C. & Williams, S. E. 2007 Does size matter for dispersal distance? *Global Ecology and Biogeography* **16**, 415-425.
Jenkins, D. G., Carey, M., Czerniewska, J., Fletcher, J., Hether, T., Jones, A., Knight, S., Knox, J., Long, T., Mannino, M., McGuire, M., Riffle, A., Segelsky, S., Shappell, L., Sterner, A., Strickler, T. & Tursi, R. 2010 A meta-analysis of isolation by distance: relic or reference standard for landscape genetics? *Ecography* **33**, 315-320.
Jetz, W. & Rahbek, C. 2001 Geometric constraints explain much of the species richness pattern in African birds. *Proceedings of the National Academy of Sciences of the United States of America* **98**, 5661-5666.
Jetz, W. & Rahbek, C. 2002 Geographic range size and determinants of avian species richness. *Science* **297**, 1548-1551.
Jones, K. E., Sechrest, W. & Gittleman, J. L. 2005 Age and area revisited: identifying global patterns and implications for conservation. In *Phylogeny and Conservation* (ed. A. Purvis, J. L. Gittleman & T. M. Brooks), pp. 141-165. Cambridge: Cambridge University Press.
Kellermann, V., van Heerwaarden, B., Sgro, C. M. & Hoffmann, A. A. 2009 Fundamental evolutionary limits in ecological traits drive Drosophila species distributions. *Science* **325**, 1244-1246.
Kendall, D. G. 1948 On the generalized birth-and-death process. *Annals of Mathematical Statistics* **19**, 1-15.
Kimura, M. & Weiss, G. H. 1964 The stepping stone model of population structure and the decarese in genetic correlation with distance. *Genetics* **49**, 561-576.
Kirkpatrick, M. & Barton, N. H. 1997 Evolution of a species' range. *American Naturalist* **150**, 1-23.

Kisel, Y. & Barraclough, T. G. 2010 Speciation has a spatial scale that depends on levels of gene flow. *American Naturalist* **175**, 316-334.
Kissling, W. D. & Carl, G. 2008 Spatial autocorrelation and the selection of simultaneous autoregressive models. *Global Ecology and Biogeography* **17**, 59-71.
Koen, E. L., Garroway, C. J., Wilson, P. J. & Bowman, J. 2010 The effect of map boundary on estimates of landscape resistance to animal movement. *pLOS ONE* **5**, 1-8.
Kozak, K. H. & Wiens, J. J. 2006 Does niche conservatism promote speciation? A case study in North American salamanders. *Evolution* **60**, 2604-2621.
Kraft, N. J. B., Cornwell, W. K., Webb, C. O. & Ackerly, D. D. 2007 Trait evolution, community assembly, and the phylogenetic structure of ecological communities. *American Naturalist* **170**, 271-283.
Kumar, S., Tamura, K. & Nei, M. 2004 MEGA3: Integrated software for molecular evolutionary genetics analysis and sequence alignment. *Briefings Bioinformatics* **5**, 150-163.
Kunin, W. E. 1998 Extrapolating species abundance across spatial scales. *Science* **281**, 1513-1515.
Lack, D. 1971 *Ecological isolation in birds*. Oxford: Blackwell.
Le Comber, S. C. & Smith, C. 2004 Polyploidy in fishes: patterns and processes. *Biological Journal of the Linnean Society* **82**, 431-442.
Lee-Yaw, J. A., Davidson, A., Mcrae, B. H. & Green, D. M. 2009 Do landscape processes predict phylogeographic patterns in the wood frog? *Molecular Ecology* **18**, 1863-1874.
Lessa, E. P., Cook, J. A. & Patton, J. L. 2003 Genetic footprints of demographic expansion in North America, but not Amazonia, during the late Quaternary. *Proceedings of the National Academy of Sciences of the United States of America* **100**, 10331-10334.
Letcher, A. J., Purvis, A., Nee, S. & Harvey, P. H. 1994 Patterns of overlap in the geographic ranges of Palearctic and British mammals. *Journal of Animal Ecology* **63**, 871-879.
Liow, L. H., Skaug, H. J., Ergon, T. & Schweder, T. 2010 Global occurrence trajectories of microfossils: environmental volatility and the rise and fall of individual species. *Paleobiology* **36**, 224-252.
Liow, L. H. & Stenseth, N. C. 2007 The rise and fall of species: implications for macroevolutionary and macroecological studies. *Proceedings of the Royal Society B-Biological Sciences* **274**, 2745-2752.
Losos, J. B. & Adler, F. R. 1995 Stumped by trees - a generalized null model for patterns of organismal diversity. *American Naturalist* **145**, 329-342.
Losos, J. B. & Glor, R. E. 2003 Phylogenetic comparative methods and the geography of speciation. *Trends in Ecology & Evolution* **18**, 220-227.
Losos, J. B., Jackman, T. R., Larson, A., de Queiroz, K. & Rodriguez-Schettino, L. 1998 Contingency and determinism in replicated adaptive radiations of island lizards. *Science* **279**, 2115-2118.
Losos, J. B. & Parent, C. E. 2009 *The speciation-area relationship*. In *The theory of island biogeography revisited* (ed Losos, J .B. & Ricklefs, R .E), pp 415-438. Princeton: Princeton University Press.

Losos, J. B. & Ricklefs, R. E. 2009 Adaptation and diversification on islands. *Science* **457**, 830-836.
Losos, J. B. & Schluter, D. 2000 Analysis of an evolutionary species-area relationship. *Nature* **408**, 847-850.
Lyons, S. K. & Willig, M. R. 1997 Latitudinal patterns of range size: Methodological concerns and empirical evaluations for New World bats and marsupials. *Oikos* **79**, 568-580.
MacArthur, J. W. & Wilson, E. O. 1967 *The theory of island biogeography*. Princeton: Princeton University Press.
MacArthur, R. H. 1972 *Geographical ecology: Patterns in the distributions of species*. New York: Harper and Row.
Maceachren, A. M. 1985 Compactness of geographic shape - comparison and evaluation of measures. *Geografiska Annaler Series B-Human Geography* **67**, 53-67.
Magallon, S. & Sanderson, M. J. 2001 Absolute diversification rates in angiosperm clades. *Evolution* **55**, 1762-1780.
Manne, L. L., Brooks, T. M. & Pimm, S. L. 1999 Relative risk of extinction of passerine birds on continents and islands. *Nature* **399**, 258-261.
Martin, P. R. & McKay, J. K. 2004 Latitudinal variation in genetic divergence of populations and the potential for future speciation. *Evolution* **58**, 938-945.
Maurer, B. A. 1994 *Geographical population analysis: tools for the analysis of biodiversity* Cambridge, MA: Blackwell Science.
Mayr, E. 1942 *Systematics and the origin of species*. New York: Columbia University Press.
Mayr, E. 1947 Ecological factors in speciation. *Evolution* **1**, 263-288.
Mayr, E. 1963 *Animal Species and Evolution*. Harvard: Belknap Press.
Mayr, E. 1982 Processes of speciation in animals. In *Mechanisms of speciation* (ed. C. Barigozzi), pp. 1-19. New York: Alan R. Liss.
McGarigal, K. & Marks, B. J. 1995 FRAGSTATS: spatial pattern analysis program for quantifying landscape structure. In *U.S. Department of Agriculture, Forest Service, Pacific Northwest Research Station*, pp. 122.
McInnes, L., Purvis, A. & Orme, C. D. L. 2009 Where do species' geographic ranges stop and why? Landscape impermeability and the Afrotropical avifauna. *Proceedings of the Royal Society B-Biological Sciences* **276**, 3063-3070.
McPeek, M. A. 2008 The Ecological Dynamics of Clade Diversification and Community Assembly. *American Naturalist* **172**, E270-E284.
McRae, B. H. 2006 Isolation by resistance. *Evolution* **60**, 1551-1561.
McRae, B. H. & Beier, P. 2007 Circuit theory predicts gene flow in plant and animal populations. *Proceedings of the National Academy of Sciences of the United States of America* **104**, 19885-19890.
Merriam, C. H. 1894 Laws of temperature control of the geographic distribution of terrestrial animals and plants. *National Geographic* **6**, 229-238.
Mittelbach, G. G., et al 2007 Evolution and the latitudinal diversity gradient: speciation, extinction and biogeography. *Ecology Letters* **10**, 315-331.
Mooers, A. O. 1995 Tree balance and tree completeness. *Evolution* **49**, 379-384.
Mooers, A. O., Harmon, L. J., Blum, M. G. B., Wong, D. H. J. & Heard, S. B. 2007 Some models of phylogenetic tree shape. In *Reconstructing evolution: new*

mathematical and computational advances (ed. O. Gascuel & M. Steel), pp. 149-163. Oxford: Oxford University Press.
Mooers, A. O. & Heard, S. B. 1997 Inferring evolutionary process from phylogenetic tree shape *Quarterly Review of Biology* **72**, 31-54.
Moore, B. R. & Donoghue, M. J. 2007 Correlates of diversification in the plant clade Dipsacales: Geographic movement and evolutionary innovations. **170**, 28-55.
Morjan, C. L. & Rieseberg, L. H. 2004 How species evolve collectively: implications of gene flow and selection for the spread of advantageous alleles. *Molecular Ecology* **13**, 1341-1356.
Nee, S. 2001 Inferring speciation rates from phylogenies. *Evolution* **55**, 661-668.
Nee, S. 2006 Birth-death models in macroevolution. *Annual Review of Ecology Evolution and Systematics* **37**, 1-17.
Nee, S., May, R. M. & Harvey, P. H. 1994 The reconstructed evolutionary process. *Philosophical Transactions of the Royal Society of London Series B-Biological Sciences* **344**, 305-311.
Nee, S., Mooers, A. O. & Harvey, P. H. 1992 Tempo and mode of evolution revealed from molecular phylogenies. *Proceedings of the National Academy of Sciences of the United States of America* **89**, 8322-8326.
New, M., Lister, D., Hulme, M. & Makin, I. 2002 A high-resolution data set of surface climate over global land areas. *Climate Research* **21**, 1-25.
Niemi, R. G., Grofman, B., Carlucci, C. & Hofeller, T. 1990 Measuring compactness and the role of a compactness standard in a test for partisan and racial gerrymandering. *Journal of Politics* **52**, 1155-1181.
Olson, D. M., Dinerstein, E., Wikramanayake, E. D., Burgess, N. D., Powell, G. V. N., Underwood, E. C., D'Amico, J. A., Itoua, I., Strand, H. E., Morrison, J. C., Loucks, C. J., Allnutt, T. F., Ricketts, T. H., Kura, Y., Lamoreux, J. F., Wettengel, W. W., Hedao, P. & Kassem, K. R. 2001 Terrestrial ecoregions of the worlds: A new map of life on Earth. *Bioscience* **51**, 933-938.
Orme, C. D. L., Davies, R. G., Burgess, M., Eigenbrod, F., Pickup, N., Olson, V. A., Webster, A. J., Ding, T. S., Rasmussen, P. C., Ridgely, R. S., Stattersfield, A. J., Bennett, P. M., Blackburn, T. M., Gaston, K. J. & Owens, I. P. F. 2005 Global hotspots of species richness are not congruent with endemism or threat. *Nature* **436**, 1016-1019.
Orme, C. D. L., Davies, R. G., Olson, V. A., Thomas, G. H., Ding, T. S., Rasmussen, P. C., Ridgely, R. S., Stattersfield, A. J., Bennett, P. M., Owens, I. P. F., Blackburn, T. M. & Gaston, K. J. 2006 Global patterns of geographic range size in birds. *Plos Biology* **4**, 1276-1283.
Owens, I. P. F., Bennett, P. M. & Harvey, P. H. 1999 Species richness among birds: body size, life history, sexual selection or ecology? *Proceedings of the Royal Society of London Series B-Biological Sciences* **266**, 933-939.
Pagel, M. 1999 Inferring the historical patterns of biological evolution. *Nature* **401**, 877-884.
Parmesan, C., Gaines, S., Gonzalez, L., Kaufman, D. M., Kingsolver, J., Townsend Peterson, A. & Sagarin, R. 2005 Empirical perspectives on species borders: from traditional biogeography to global change. *Oikos* **108**, 58-75.

Paul, J. R., Morton, C., Taylor, C. M. & Tonsor, S. J. 2009 Evolutionary time for dispersal limits the extent but not the occupancy of species' potential ranges in the tropical plant genus Psychotria (Rubiaceae). *American Naturalist* **173**, 188-199.

Payne, J. L. & Finnegan, S. 2007 The effect of geographic range on extinction risk during background and mass extinction. *Proceedings of the National Academy of Sciences of the United States of America* **104**, 10506-10511.

Peterson, A. T., Barve, N., Bini, L. M., Diniz-Filho, J. A., Jimenez-Valverde, A., Lira-Noriegaa, A., Lobo, J., Maher, S., de Marco, P., Martinez-Meyer, E., Nakazawa, Y. & Soberon, J. 2009 The climate envelope may not be empty. *Proceedings of the National Academy of Sciences of the United States of America* **106**, E47-E47.

Peterson, M. A. & Denno, R. F. 1998 The influence of dispersal and diet breadth on patterns of genetic isolation by distance in phytophagous insects. *American Naturalist* **152**, 428-446.

Phillimore, A. B., Freckleton, R. P., Orme, C. D. L. & Owens, I. P. F. 2006 Ecology predicts large-scale patterns of phylogenetic diversification in birds. *American Naturalist* **168**, 220-229.

Phillimore, A. B., Orme, C. D. L., Davies, R. G., Hadfield, J. D., Reed, W. J., Gaston, K. J., Freckleton, R. P. & Owens, I. P. F. 2007 Biogeographical basis of recent phenotypic divergence among birds: A global study of subspecies richness. *Evolution* **61**, 942-957.

Phillimore, A. B., Orme, C. D. L., Thomas, G. H., Blackburn, T. M., Bennett, P. M., Gaston, K. J. & Owens, I. P. F. 2008 Sympatric speciation in birds is rare: Insights from range data and simulations. *American Naturalist* **171**, 646-657.

Phillimore, A. B. & Price, T. D. 2008 Density-dependent cladogenesis in birds. *Plos Biology* **6**, 483-489.

Phillimore, A. B. & Price, T. D. 2009 Ecological influences on the temporal pattern of speciation. In *Speciation and patterns of diversity* (ed. R. Butlin, J. Bridle & D. Schluter). pp 240-256. Cambridge: Cambridge University Press.

Pinto, G., Mahler, D. L., Harmon, L. J. & Losos, J. B. 2008 Testing the island effect in adaptive radiation: rates and patterns of morphological diversification in Caribbean and mainland Anolis lizards. *Proceedings of the Royal Society B-Biological Sciences* **275**, 2749-2757.

Pocock, M. J. O., Hartley, S., Telfer, M. G., Preston, C. D. & Kunin, W. E. 2006 Ecological correlates of range structure in rare and scarce British plants. *Journal of Ecology* **94**, 581-596.

Powell, M. G. 2007 Geographic range and genus longevity of late Paleozoic brachiopods. *Paleobiology* **33**, 530-546.

Price, T. 2008 *Speciation In Birds*. Colorado: Roberts and Company.

Price, T. D. & Kirkpatrick, M. 2009 Evolutionarily stable range limits set by interspecific competition. *Proceedings of the Royal Society B-Biological Sciences* **276**, 1429-1434.

Pulliam, H. R. 2000 On the relationship between niche and distribution. *Ecology Letters* **3**, 349-361.

Purvis, A. & Agapow, P. M. 2002 Phylogeny imbalance: Taxonomic level matters. *Systematic Biology* **51**, 844-854.

Purvis, A., Gittleman, J. L., Cowlishaw, G. & Mace, G. M. 2000 Predicting extinction risk in declining species. *Proceedings of the Royal Society B-Biological Sciences* **267**, 1947-1952.

Purvis, A., Orme, C. D. L., Toomey, N. H. & Pearson, P. N. 2009 Temporal patterns in diversification rates. In *Speciation and patterns of diversity* (ed. R. Butlin, J. Bridle & D. Schluter). pp 278-300. Cambridge: Cambridge University Press.

Pybus, O. G. & Harvey, P. H. 2000 Testing macro-evolutionary models using incomplete molecular phylogenies. *Proceedings of the Royal Society of London Series B-Biological Sciences* **267**, 2267-2272.

Rabosky, D. L. 2009a Ecological limits and diversification rate: alternative paradigms to explain the variation in species richness among clades and regions. *Ecology Letters* **12**, 735-743.

Rabosky, D. L. 2009b Ecological Limits on Clade Diversification in Higher Taxa. *American Naturalist* **173**, 662-674.

Rabosky, D. L. & Lovette, I. J. 2008 Density-dependent diversification in North American wood warblers. *Proceedings of the Royal Society B-Biological Sciences* **275**, 2363-2371.

Rahbek, C. 2005 The role of spatial scale and the perception of large-scale species-richness patterns. *Ecology Letters* **8**, 224-239.

Rahbek, C., Gotelli, N. J., Colwell, R. K., Entsminger, G. L., Rangel, T. F. L. V. B. & Graves, G. R. 2007 Predicting continental-scale patterns of bird species richness with spatially explicit models. *Proceedings of the Royal Society B-Biological Sciences* **274**, 165-174.

Rahbek, C. & Graves, G. R. 2001 Multiscale assessment of patterns of avian species richness. *Proceedings of the National Academy of Sciences of the United States of America* **98**, 4534-4539.

Raikow, R. J. 1986 Why are there so many kinds of passerine birds? *Systematic Zoology* **35**, 255-259.

Rambaut, A. & Drummond, A. J. 2007 Tracer v1.4.

Rangel, T. F. L. V. B. & Diniz-Filho, J. A. F. 2005 An evolutionary tolerance model explaining spatial patterns in species richness under environmental gradients and geometric constraints. *Ecography* **28**, 253-263.

Rangel, T. F. L. V. B., Diniz-Filho, J. A. F. & Colwell, R. K. 2007 Species richness and evolutionary niche dynamics: A spatial pattern-oriented simulation experiment. *American Naturalist* **170**, 602-616.

Rapoport, E. H. 1982 *Areography: Geographical strategies of species*. New York: Pergamon Press.

Raup, D. M. 1985 Mathematical-models of cladogenesis. *Paleobiology* **11**, 42-52.

Raup, D. M., Gould, S. J., Schopf, T. J. M. & Simberloff, D. S. 1973 Stochastic models of phylogeny and the evolution of diversity. *Journal of Geology* **81**, 525-542.

Ree, R. H., Moore, B. R., Webb, C. O. & Donoghue, M. J. 2005 A likelihood framework for inferring the evolution of geographic range on phylogenetic trees. *Evolution* **59**, 2299-2311.

Ree, R. H. & Smith, S. A. 2008 Maximum likelihood inference of geographic range evolution by dispersal, local extinction, and cladogenesis. *Systematic Biology* **57**, 4-14.

Remsen, J. V. & Parker, T. A. 1983 Contribution of river-created habitats to bird species richness in Amazonia. *Biotropica* **15**, 223-231.
Revell, L. J., Harmon, L. J. & Collar, D. C. 2008 Phylogenetic signal, evolutionary process, and rate. *Systematic Biology* **57**, 591-601.
Ricklefs, R. E. 2003 Global diversification rates of passerine birds. *Proceedings of the Royal Society of London Series B-Biological Sciences* **270**, 2285-2291.
Ricklefs, R. E. 2004 Cladogenesis and morphological diversification in passerine birds. *Nature* **430**, 338-341.
Ricklefs, R. E. 2005 Small clades at the periphery of passerine morphological space. *American Naturalist* **165**, 43-659.
Ricklefs, R. E. 2006a Global variation in the diversification rate of passerine birds. *Ecology* **87**, 2468-2478.
Ricklefs, R. E. 2006b The unified neutral theory of biodiversity: Do the numbers add up? *Ecology* **87**, 1424-1431.
Ricklefs, R. E. 2007 Estimating diversification rates from phylogenetic information. *Trends in Ecology & Evolution* **22**, 601-610.
Ricklefs, R. E. 2008 Disintegration of the ecological community. *American Naturalist* **172**, 741-750.
Ricklefs, R. E. 2010 Evolutionary diversification, coevolution between populations and their antagonists, and the filling of niche space. *Proceedings of the National Academy of Sciences of the United States of America* **107**, 1265-1272.
Ricklefs, R. E. 2011 Applying a regional community concept to forest birds of eastern North America. *Proceedings of the National Academy of Sciences of the United States of America* **108**, 2300-2305.
Ricklefs, R. E. & Bermingham, E. 1999 Taxon cycles in the Lesser Antillean avifauna. *Ostrich* **70**, 49-59.
Ricklefs, R. E. & Bermingham, E. 2002 The concept of the taxon cycle in biogeography. *Global Ecology and Biogeography* **11**, 353-361.
Ricklefs, R. E. & Cox, G. W. 1972 Taxon cycles in West-Indian avifauna. *American Naturalist* **106**, 195-219.
Ricklefs, R. E. & Latham, R. E. 1992 Intercontinental correlation of geographical ranges suggests stasis in ecological traits of relict genera of temperate perennial herbs. *American Naturalist* **139**, 1305-1321.
Rogers, J. S. 1996 Central moments and probability distributions of three measures of phylogenetic tree imbalance. *Systematic Biology* **45**, 99-110.
Romdal, T. S., Colwell, R. K. & Rahbek, C. 2005 The influence of band sum area, domain extent, and range sizes on the latitudinal mid-domain effect. *Ecology* **86**, 235-244.
Root, T. 1988a Energy constraints on avian distributions and abundances. *Ecology* **69**, 330-339.
Root, T. 1988b Environmental-factors associated with avian distributional boundaries. *Journal of Biogeography* **15**, 489-505.
Rosenzweig, M. L. 1975 On continental steady states of species diversity. In *The Ecology and Evolution of Communities* (ed. M. Cody & J. M. Diamond). pp 121-141. Harvard: Harvard University Press.

Rosenzweig, M. L. 1978 Geographical speciation: on range size and the probability of isolate formation In *Proceedings of the Washington State University Conference on Biomathematics and Biostatistics* (ed. D. Wolkind), pp. 172-194. Washington State University: Pullman.
Rosenzweig, M. L. 1995 *Species diversity in space and time*. Cambridge: Cambridge University Press
Rosindell, J. & Cornell, S. J. 2009 Species-area curves, neutral models, and long-distance dispersal. *Ecology* **90**, 1743-1750.
Rosindell, J., Cornell, S. J., Hubbell, S. P. & Etienne, R. S. 2010 Protracted speciation revitalizes the neutral theory of biodiversity. *Ecology Letters* **13**, 716-727.
Rousset, F. 1997 Genetic differentiation and estimation of gene flow from F-statistics under isolation by distance. *Genetics* **145**, 1219-1228.
Ruggiero, A. 2001 Size and shape of the geographical ranges of Andean passerine birds: spatial patterns in environmental resistance and anisotropy. *Journal of Biogeography* **28**, 1281-1294.
Ruggiero, A., Lawton, J. H. & Blackburn, T. M. 1998 The geographic ranges of mammalian species in South America: spatial patterns in environmental resistance and anisotropy. *Journal of Biogeography* **25**, 1093-1103.
Rundell, R. J. & Price, T. D. 2009 Adaptive radiation, nonadaptive radiation, ecological speciation and nonecological speciation. *Trends in Ecology & Evolution* **24**, 394-399.
Rundle, H. D. & Nosil, P. 2005 Ecological speciation. *Ecology Letters* **8**, 336-352.
Russell, R., Wood, S. A., Allison, G. & Menge, B. A. 2006 Scale, environment, and trophic status: The context dependency of community saturation in rocky intertidal communities. *American Naturalist* **167**, E158-E170.
Sandel, B. 2009 Geometric constraint model selection - an example with New World birds and mammals. *Ecography* **32**, 1001-1010.
Schipper, J. et al. 2008 The status of the world's land and marine mammals: Diversity, threat, and knowledge. *Science* **322**, 225-230.
Schluter, D. 2000 *The ecology of adaptive radiation*. Oxford: Oxford University Press.
Schluter, D. 2001 Ecology and the origin of species. *Trends in Ecology & Evolution* **16**, 372-380.
Schluter, D. 2009 Evidence for ecological speciation and its alternative. *Science* **323**, 737-741.
Schluter, D. & Conte, G. L. 2009 Genetics and ecological speciation. *Proceedings of the National Academy of Sciences of the United States of America* **106**, 9955-9962.
Seehausen, O. 2006 African cichlid fish: a model system in adaptive radiation research. *Proceedings of the Royal Society B-Biological Sciences* **273**, 1987-1998.
Sexton, J. P., McIntyre, P. J., Angert, A. L. & Rice, K. J. 2009 Evolution and ecology of species range limits. *Annual Review of Ecology Evolution and Systematics* **40**, 415-436.
Sibley, C. G. & Monroe, B. L. 1990 *Distribution and Taxonomy of the Birds of the World*. New Haven: Yale University Press.
Simpson, G. G. 1953 *The major features of evolution*. New York: Columbia University Press.
Skellam, J. G. 1951 Random dispersal in theoretical populations *Biometrika* **38**, 196-218.

Slatkin, M. 1993 Isolation by distance in equilibrium and nonequilibrium populations. *Evolution* **47**, 264-279.
Slatkin, M. & Maddison, W. P. 1990 Detecting isolation by distance using phylogenies of genes. *Genetics* **126**, 249-260.
Slowinski, J. B. & Guyer, C. 1989 Testing the stochasticity of patterns of organismal diversity - an improved null model. *American Naturalist* **134**, 907-921.
Slowinski, J. B. & Guyer, C. 1993 Testing whether certain traits have caused amplified diversification - an improved method based on a model of random speciation and extinction. *American Naturalist* **142**, 1019-1024.
Stanley, S. M. 1979 *Macroevolution: pattern and process*. San Fransisco: W. H. Freeman.
Steeman, M. E., Hebsgaard, M. B., Fordyce, E., Ho, S. Y. W., Rabosky, D. L., Nielsen, R., Rahbek, C., Glenner, H., Sorensen, M. V. & Willerslev, E. 2009 Radiation of extant cetaceans driven by restructuring of the oceans. *Systematic Biology* **58**, 573-585.
Storch, D., Davies, R. G., Zajicek, S., Orme, C. D. L., Olson, V., Thomas, G. H., Ding, T. S., Rasmussen, P. C., Ridgely, R. S., Bennett, P. M., Blackburn, T. M., Owens, I. P. F. & Gaston, K. J. 2006 Energy, range dynamics and global species richness patterns: reconciling mid-domain effects and environmental determinants of avian diversity. *Ecology Letters* **9**, 1308-1320.
Stuart-Fox, D. & Owens, I. P. F. 2003 Species richness in agamid lizards: chance, body size, sexual selection or ecology? *Journal of Evolutionary Biology* **16**, 659-669.
Stuart, S. N., Chanson, J. S., Cox, N. A., Young, B. E., Rodrigues, A. S. L., Fischman, D. L. & Waller, R. W. 2004 Status and trends of amphibian declines and extinctions worldwide. *Science* **306**, 1783-1786.
Sutherland, G. D., Harestad, A. S., Price, K. & Lertzman, K. P. 2000 Scaling of natal dispersal distances in terrestrial birds and mammals. *Conservation Ecology* **4**, 16.
Terborgh, J. 1973 Notion of favorableness in plant ecology. *American Naturalist* **107**, 481-501.
Terborgh, J. 1985 The role of ecotones in the distribution of Andean birds. *Ecology* **66**, 1237-1246.
Terborgh, J. & Weske, J. S. 1975 Role of competition in distribution of Andean birds. *Ecology* **56**, 562-576.
Thompson, J. N. 2005 *The geographic mosaic of coevolution* Chicago: University of Chicago Press.
Udvardy, M. D. F. 1969 *Dynamic Zoogeography: with special reference to land animals*. New York: Van Nostrand Reinhold Company.
Vamosi, J. C. & Vamosi, S. M. 2010 Key innovations within a geographical context in flowering plants: towards resolving Darwin's abominable mystery. *Ecology Letters* **13**, 1270–1279.
Vermeij, G. J. 1987 The dispersal barrier in the tropical Pacific - implications for molluscan speciation and extinction. *Evolution* **41**, 1046-1058.
Via, S. 2001 Sympatric speciation in animals: the ugly duckling grows up. *Trends in Ecology & Evolution* **16**, 381-390.
Waldron, A. 2007 Null models of geographic range size evolution reaffirm its heritability. *American Naturalist* **170**, 221-231.

Webb, T. J. & Gaston, K. J. 2000 Geographic range size and evolutionary age in birds. *Proceedings of the Royal Society of London Series B-Biological Sciences* **267**, 1843-1850.
Webb, T. J., Kershaw, M. & Gaston, K. J. 2001 Rarity and phylogeny in birds. In *Biotic homogenisation* (ed. J. Lockwood & M. L. McKinney), pp. 61-84. New York: Kluwer Academic.
Weir, J. T. 2006 Divergent timing and patterns of species accumulation in lowland and highland neotropical birds. *Evolution* **60**, 842-855.
Weir, J. T., Bermingham, E. & Schluter, D. 2009 The Great American Biotic Interchange in birds. *Proceedings of the National Academy of Sciences of the United States of America* **106**, 21737-21742.
Weir, J. T. & Schluter, D. 2004 Ice sheets promote speciation in boreal birds. *Proceedings of the Royal Society of London Series B-Biological Sciences* **271**, 1881-1887.
Weir, J. T. & Schluter, D. 2007 The latitudinal gradient in recent speciation and extinction rates of birds and mammals. *Science* **315**, 1574-1576.
Weir, J. T. & Schluter, D. 2008 Calibrating the avian molecular clock. *Molecular Ecology* **17**, 2321-2328.
Welch, J. J., Bininda-Emonds, O. R. P. & Bromham, L. 2008 Correlates of substitution rate variation in mammalian protein-coding sequences. *Bmc Evolutionary Biology* **8**, 53.
Whitlock, M. C. & McCauley, D. E. 1999 Indirect measures of gene flow and migration: F-ST not equal 1/(4Nm+1). *Heredity* **82**, 117-125.
Wiens, J. J. 2004 Speciation and ecology revisited: phylogenetic niche conservatism and the origin of species *Evolution* **58**, 193–197.
Wiens, J. J. & Donoghue, M. J. 2004 Historical biogeography, ecology and species richness. *Trends in Ecology & Evolution* **19**, 639-644.
Willis, J. C. 1922 *Age and area*. Cambridge: Cambridge University Press.
Wilson, D. E. & Reeder, D. M. (ed.) 2005 *Mammal species of the world: A taxonomic and geographic reference*. Baltimore: Johns Hopkins University Press.
Wilson, E. O. 1961 The nature of the taxon cycle in the Melanesian ant fauna. *The American Naturalist* **95**, 169-193.
Wilson, R. J., Thomas, C. D., Fox, R., Roy, D. B. & Kunin, W. E. 2004 Spatial patterns in species distributions reveal biodiversity change. *Nature* **432**, 393-396.
Wright, S. 1941 The "age and area" concept extended. *Ecology* **22**, 345-347.
Wright, S. 1943 Isolation by distance. *Genetics* **28**, 114-138.
Yule, U. 1925 A mathematical theory of evolution, based on the conclusions of Dr J. C. Willis, F.R.S. *Philosophical Transactions of the Royal Society of London Series B-Biological Sciences* **213**, 21-87.
Zink, R. M. & Barrowclough, G. F. 2008 Mitochondrial DNA under siege in avian phylogeography. *Molecular Ecology* **17**, 2107-2121.
Zink, R. M. & Slowinski, J. B. 1995 Evidence from molecular systematics for decreased avian diversification in the Pleistocene epoch. *Proceedings of the National Academy of Sciences of the United States of America* **92**, 5832-5835.